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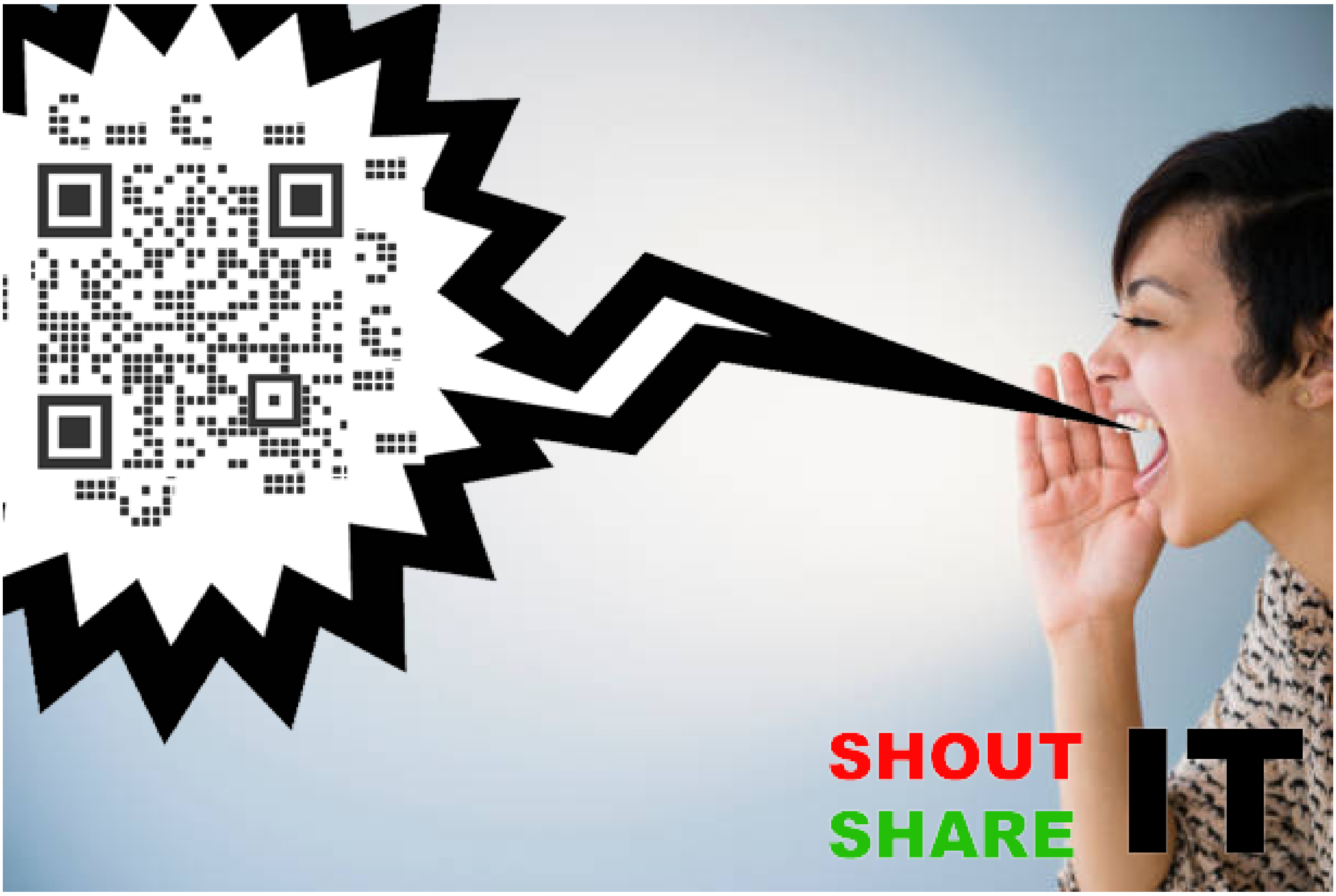
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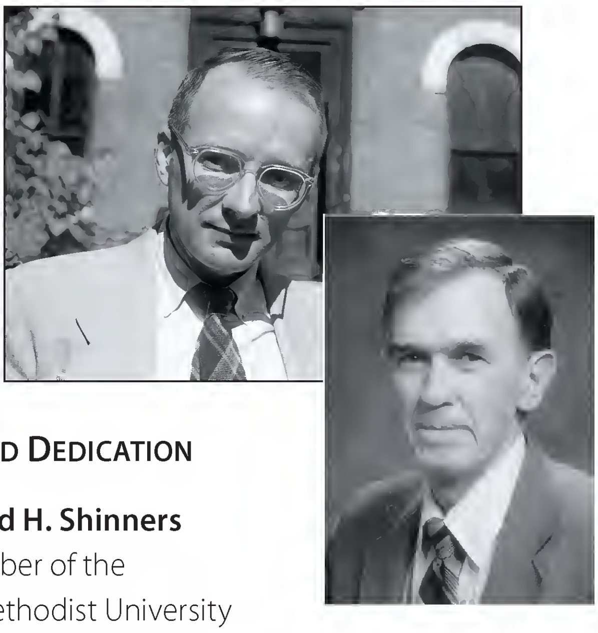

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1971—William F. Mahler (right), professor of botany at SMU and director emeritus of BRIT, inherited editorship and copyright.

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Electronically tinted botanical illustration of *Liatris aestivalis* originally used on BRIT's anniversary poster 2001. Summer gayfeather flowers mid Jul–Aug(–Sep) and is endemic to Oklahoma and Texas. Sida 19:768. 2001. Botanical illustration by Linny Heagy ©2001.

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TYPIFICATION OF *SEDUM RUBROGLAUCUM* (CRASSULACEAE)

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ABSTRACT

Sedum rubroglaucum was validly published in 1919, but the type specimen at DBN was not found. *Sedum rubroglaucum* as described, and later illustrated, can not be readily distinguished from a number of closely related taxa in *Sedum* sect. *Gormania* in the absence of a type specimen. A neotype is designated, based on a 1940 collection at YM from the type locality, in Yosemite National Park, California. *Sedum rubroglaucum* becomes a synonym of the typical expression of the widespread California species *S. obtusatum*, described in 1868.

RESUMEN

Sedum rubroglaucum se publicó válidamente en 1919, pero el espécimen tipo de DBN no se encontró. *Sedum rubroglaucum* tal como se describió, y posteriormente se ilustró, no puede distinguirse fácilmente de un número de taxa relacionados de *Sedum* sect. *Gormania* en ausencia de un specimen tipo. Se designa un neotipo, basado en una colección de 1940 en YM de la localidad tipo, en Yosemite National Park, California. *Sedum rubroglaucum* se hace sinónimo la especie típica y extendida por California *S. obtusatum*, descrita en 1868.

INTRODUCTION

Sedum L. sect. *Gormania* (Britton) R.T. Clausen is a small group of perennial species in California and Oregon, with persistent rosettes on the flowering shoots, and corollas that are fused a short distance above the base. One member of sect. *Gormania* is *S. rubroglaucum* Praeger. The name was validly published (Praeger 1919) but lacks a type, as Praeger's original material is missing. According to Stafleu and Cowan (1983), Praeger's types and the majority of his herbarium specimens were deposited in Dublin, Ireland, at DBN, with additional material at A, BEL, BM, CGE, E, GH, ILL, K, LIV, and NOT (herbarium acronyms in Thiers, continuously updated). A search of those institutions failed to yield any collections labeled *Sedum rubroglaucum*.

Praeger (1919) cited a single gathering, which must be interpreted as the type. *Sedum rubroglaucum* was described from living material sent to Praeger from California, on the Short Trail [now known as the Four Mile Trail] in Yosemite National Park, California. Praeger (1919) said: "The plant was collected and forwarded alive by Prof. H.M. Hall in June, 1915, and flowered in the following year." There is no surviving specimen to serve as holotype, as no original material from Praeger or Hall is extant. Jepson (1936:110) cited a specimen by Hall as the type of *S. rubroglaucum*, but there is no indication that he saw a herbarium sheet. It is more likely Jepson was citing the solitary collection mentioned in Praeger's 1919 protologue. Hall was based in California. A physical search in California collections was unsuccessful; there were no 1915 *Sedum* sect. *Gormania* vouchers prepared by H.M. Hall at CAS, DS, GH, JEPS, POM, RSA, or UC. A wider search in the database of the Consortium of California Herbaria (2015) yielded 331 Hall specimens gathered in 1915 in California, none were in the genus *Sedum*. Clausen (1975) was also unable to locate specimens that Praeger might have had at hand when describing *S. rubroglaucum*. Hall's 1915 shipment to Praeger did not include flowering material, diminishing the chances he would have retained a pressed duplicate in a California herbarium. Praeger (1919) noted the living specimen bloomed in September 1916 in a garden, and a flowering shoot was eventually illustrated for Praeger's (1921:219, fig. 125) catalogue of cultivated *Sedum*. Is the 1921 illustration (see Fig. 1) appropriate as a lectotype for the name *S. rubroglaucum*, in the absence of a holotype specimen? Apparently not, for the artist may have worked after 1919. If the graphic was published in 1919, it would qualify as part of Praeger's original materials at the time of publication. But Praeger used the artwork in 1921, weakening the argument it was

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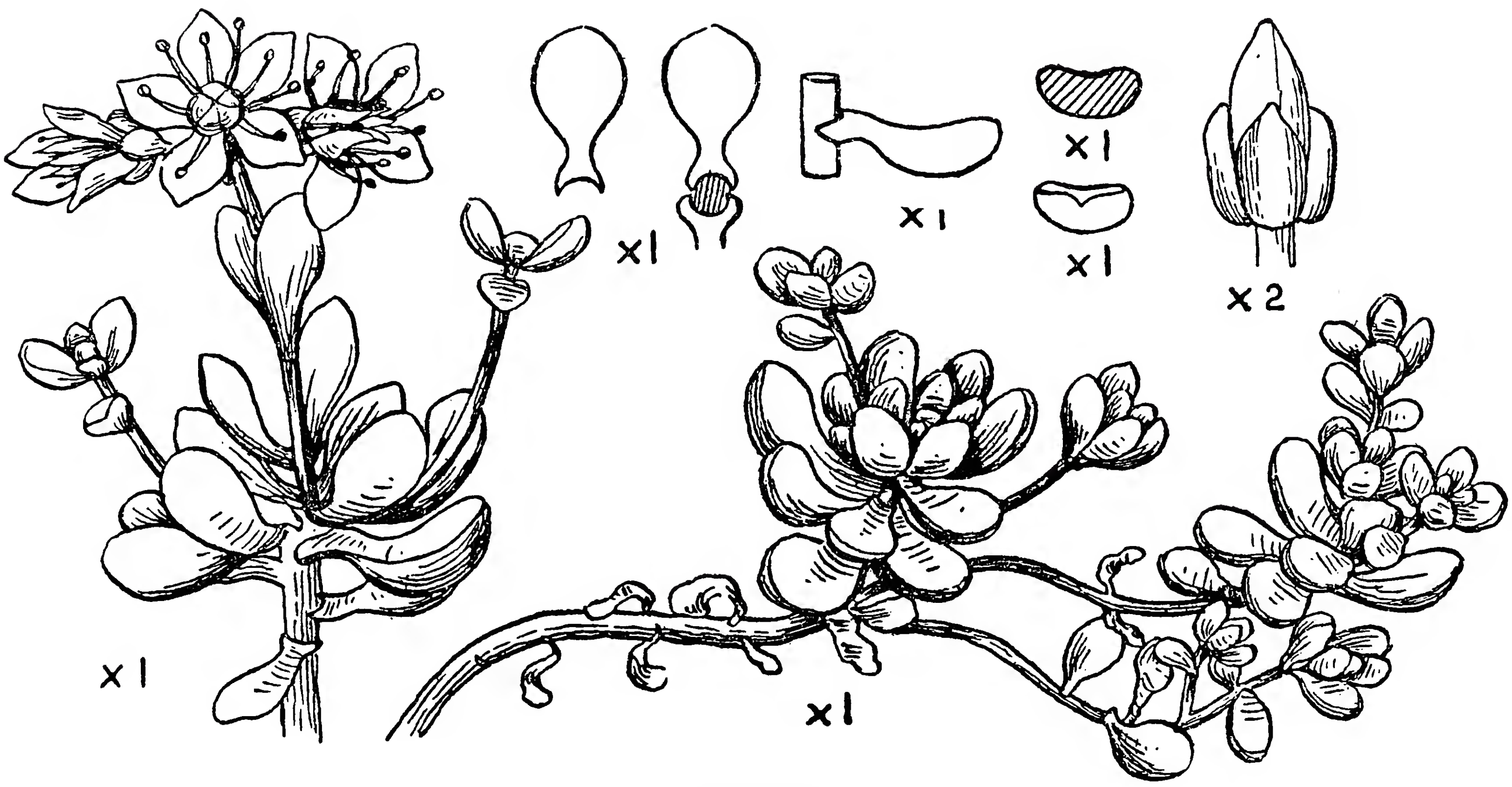


FIG. 125.—*S. rubroglaucum* Praeger.

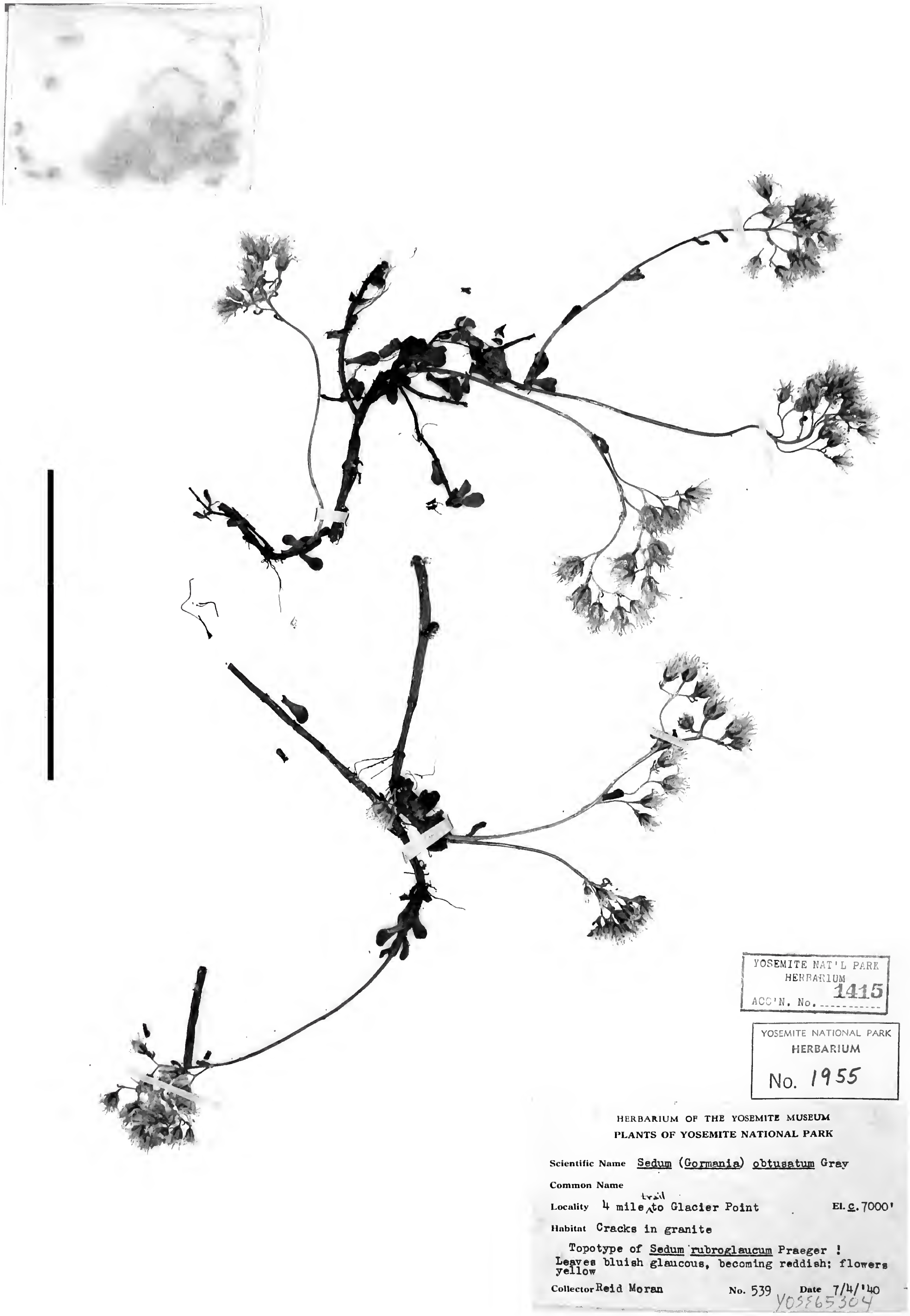
FIG. 1. *Sedum rubroglaucum*, illustrated by Praeger (1921:219, fig. 125) two years after publication of the binomial. Reproduced with permission of *The Garden* (formerly *The Journal of the Royal Horticultural Society*).

original material, suitable for lectotype designation, in the sense of Articles 9.2 and 9.3 of the Melbourne Code (McNeill et al. 2012).

The protologue of *Sedum rubroglaucum* mentions the petals are fused at the base, and Praeger (1919, 1921) placed it appropriately in *Sedum* sect. *Gormania*. The only illustration (Fig. 1) also shows a typical member of the section with rosettes on the flowering and sterile shoots. However, neither the 1921 illustration nor the 1919 description are sufficient to distinguish *S. rubroglaucum* from several other closely related California taxa more recently described in sect. *Gormania*, such *S. albomarginatum* R.T. Clausen, *S. oblanceolatum* R.T. Clausen, and the four subspecies of *S. obtusatum* A. Gray treated in Boyd and Denton (2012).

Clausen (1975:371) deduced that *Sedum rubroglaucum* must refer to nomenclaturally typical material of *S. obtusatum*, based on geography, and that was a reasonable assumption. According to Taylor (2010), only two perennial rosette-forming *Sedum* species are present in Yosemite National Park, *S. obtusatum* and *S. spathulifolium* Hook. The latter, including its synonym *S. yosemitense* Britton, has petals separated to the base, not fused, and so differs from the 1919 description of *S. rubroglaucum*. Therefore, based on the locality and the protologue, there seems little doubt that the material sent by Hall to Praeger was the typical subspecies of *S. obtusatum*, following current classifications of the genus (Clausen 1975; Denton 1982, 1993; Ohba 2009; Boyd & Denton 2012; Wilson et al. 2014; Zika 2014).

The 1919 description of *Sedum rubroglaucum* is ambiguous, as is the 1921 illustration, and neither are supported by an extant specimen. Thus a neotype is designated below, in accordance with Articles 9.7 and 9.13 of the Code. The neotype specimen (Fig. 2) is housed at the herbarium of Yosemite National Park, and was collected by Reid Moran in 1940 from the same trail where Hall made his collection in 1915. Moran stated on his specimen label: "... 'topotype' of *Sedum rubroglaucum*." This choice of neotype is consistent with both Praeger's concept and locality, and fixes *S. rubroglaucum* as a synonym of the typical expression of *S. obtusatum*, a name with priority, published by Asa Gray (1868).



YOSEMITE NAT'L PARK
HERBARIUM
ACC'N. No. 1415

YOSEMITE NATIONAL PARK
HERBARIUM
No. 1955

HERBARIUM OF THE YOSEMITE MUSEUM
PLANTS OF YOSEMITE NATIONAL PARK

Scientific Name Sedum (Gormania) obtusatum Gray
Common Name
Locality 4 mile trail to Glacier Point El. c. 7000'
Habitat Cracks in granite
Topotype of Sedum rubroglaucum Praeger !
Leaves bluish glaucous, becoming reddish; flowers yellow
Collector Reid Moran No. 539 Date 7/4/'40
YOS565304

Fig. 2. *Sedum rubroglaucum* neotype, *Moran 539* (YM). Scale bar 10 cm. Reproduced with permission of the Yosemite Museum Herbarium, U.S. National Park Service.

TAXONOMY

Sedum rubroglaucum Praeger, J. Bot. 57:51. 1919. (**Fig. 2**). Type: U.S.A. CALIFORNIA [Mariposa Co.]: Yosemite National Park, Four Mile Trail [formerly known as Short Trail] to Glacier Point, cracks in granite, elev. ca. 7000 ft [2134 m], 4 Jul 1940, *R.V. Moran 539* (neotype, designated here: YM!, catalogue number YOSE65304, ex YM1415, ex YM1955; isoneotype: UCSB71676!).

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I am grateful to Howard Fox, Elizabeth Brennan and Aidan Diskin for their assistance in searching for Robert Lloyd Praeger and Harvey Monroe Hall materials at DBN, including the living collections of the associated garden. I extend my appreciation to the keepers and staff of all the institutions cited, for their time and effort searching for Praeger's original material. Alison Colwell examined the holdings of the herbarium of Yosemite National Park, and set aside relevant gatherings, while the Curator, Miriam Watson, granted permission to reproduce an image of the neotype. Dean Taylor provided valuable collecting notes from Hall's visit to Yosemite in May 1915. Chris Young, editor of The Garden (formerly The Journal of the Royal Horticultural Society), kindly allowed the reproduction of Praeger's 1921 illustration. I thank both John Wiersema and Kanchi Gandhi for their insights and suggested revisions. Julie Nelson of the Shasta-Trinity National Forest granted partial support for *Sedum* sect. *Gormania* research, done in conjunction with Barbara Wilson, Richard Brainerd, and Nick Otting of the Carex Working Group, and I am indebted to all of them for their lively interest in the project.

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BOOK REVIEW

Johnnie L. Gentry, George P. Johnson, Brent T. Baker, C. Theo Witsell, & Jennifer D. Ogle, eds. 2013. **Atlas of the Vascular Plants of Arkansas.** (ISBN-13: 978-0-615-67980-8, pbk). University of Arkansas, Department of Printing Services, University Services Building, 2801 S. University Ave., Little Rock, Arkansas 72204, U.S.A. (**Orders:** cavern.uark.edu/~arkflora/, herb@uark.edu, University of Arkansas Herbarium, Attn: Jennifer Ogle, Biomass Research Center 141, University of Arkansas, Fayetteville, Arkansas 72701, U.S.A., 1-479-575-4372). $43.90, 709 pp., 2892 maps, some color introduction maps, 8½" × 11".

The *Atlas of the Vascular Plants of Arkansas* is the complimentary work of the *Checklist of the Vascular Plants of Arkansas*, two critical accomplishments of the Arkansas Vascular Flora Committee (AVFC) seeking definitive documentation of the known native and naturalized vascular plant species in the state of Arkansas. The *Atlas* goes one step further than the previously-published *Checklist* by providing known county-distribution maps for every species presently known in the state. Each species reported in the atlas has one county distribution map under which the family, genus, species, and common name are listed. The maps are well-sized and are conveniently organized alphabetically by scientific name of the family, genus, species, subspecies, variety, and a few putatively-accepted hybrids under four major sections: Pteridophytes (ferns and fern allies), Gymnosperms (conifers), Angiosperm Dicots, and Angiosperm Monocots. AVFC adopts many changes in taxonomic alignments based on updated phylogenetic research and maintains that the project will update taxonomy as that research continues. The atlas portion also assigns a numerical code for species that are introduced, endemic to Arkansas, non-native invasive, and/or of special conservation concern in Arkansas.

The enormity of biogeographical information presented by this book is put into context by an excellent introduction, including information on history of documentation of the flora in the state, geology relevant to the flora, and natural vegetation. While the atlas portion itself functions well as an updated geographic record of the flora, the additional information in the introduction, atlas, and appendices converts the *Atlas* into a relevant, modern documentation of the state's natural history that provides an important baseline upon which future research will build.—*Devin Rodgers, Research Associate, Botanical Research Institute of Texas, Fort Worth, Texas, U.S.A.*

MICRANTHES RUFOPILOSA (SAXIFRAGACEAE) COMB. NOV.: AN ALPINE SPECIES FROM ALASKA AND YUKON

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ABSTRACT

Micranthes rufopilosa comb.nov. is published with comparisons to related taxa: *M. gaspensis, M. nivalis,* and *M. tenuis*.

RESUMEN

Se publica **Micranthes rufopilosa** comb. nov. con comparaciones con los taxa relacionados: *M. gaspensis*, *M. nivalis*, y *M. tenuis*.

INTRODUCTION

Micranthes rufopilosa (Hultén) D.F. Murray & Elven, comb.nov. Basionym: *Saxifraga nivalis* var. *rufopilosa* Hultén, Ark. Bot. ser. 2, 7:69. 1967 (1968), validly published in Madroño 19:223.1968. Type: U.S.A. Alaska: Steese Highway, mountains W of Mastodon Dome, *Eric Hultén s.n.*, 25–26 Jul 1964 (holotype: S!).

Saxifraga rufopilosa (Hultén) A.E. Porsild, Natl. Mus. Canad., Publ. Bot. 4:41. 1974 (1975).
Saxifraga ?eriophora sensu A.E. Porsild non S. Watson, Canad. Field-Naturalist 79:79–90. 1965.
Saxifraga tenuis sensu A.E. Porsild & Cody pro parte, Vasc. Pl. Continental NWT Canada, map 710, fide Cody, Fl. Yukon. 1996.

Micranthes rufopilosa must be discussed in the context of its largely sympatric close morphological relatives: *M. nivalis*, *M. tenuis*, and also the geographically distant *M. gaspensis*. The assertion that *M. tenuis* and *M. nivalis* are distinguished only with great difficulty (Brouillet & Elvander 2009) is not our experience. The two species are distinguished by several morphological discontinuities (e.g., Healy and Gillespie 2004).

Hultén was reluctant to recognize *M. tenuis* at a rank higher than variety. In his manual (1968a) Hultén treated the entities *tenuis* and *rufopilosa* as two varieties of *M. nivalis*. He later cited (1971) the differences between *M. tenuis* and *M. nivalis* but treated those differences as inconsistent, characterizing their occurrence as "here and there". As of 1973, he still felt that those treating the taxon *tenuis* at the rank of species did so on cytological grounds and remarked that he had not seen good material *of M. tenuis* from Alaska, where many specimens now document the species. Hultén was here not in agreement with other European authors who had recognized the two taxa as distinct species for nearly a century. However, we note, as Healy and Gillespie (2004) remarked, "typical" or "good" *M. tenuis* of Europe is not what is found in North America, at least in the western parts where Hultsén had his field experience.

After reviewing *M. tenuis* and *M. nivalis* for the Canadian Arctic, Savile (1961) concluded that in the High Arctic those two species are easily separated, but to the south those distinctions become less clear as plants somewhat intermediate can be found. Thus Savile recognized a third taxon, this one from the "Alaska-Yukon refugium" meaning the unglaciated lands there, implying that this taxon has a different distribution because it had a different history from the two species in the glaciated Canadian Arctic. His third taxon is *M. rufopilosa*.

Healy and Gillespie (2004) demonstrated in excellent detail that *M. nivalis* and *M. tenuis* from arctic Canada differ in both morphology and cpDNA. They also pointed out that the few alpine plants from Alaska and Yukon they had seen, ones they had treated as *M. tenuis,* departed from the arctic specimens of that species by quantitative characters, and these plants appeared to be intermediate between *M. nivalis* and *M. tenuis.* They too had come upon *M. rufopilosa*.

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Porsild's description of *M. tenuis* (1951) from along the Canol Road referred, we believe, to *M. rufopilosa,* which at that time neither he nor anyone else in North America recognized. In that account he emphasized the reddish pubescence on lower leaf surfaces and pink to purplish petals, two features that, in part, define *M. rufopilosa.*

Then Porsild (1965), when determining material from central Alaska, Steese Highway near Eagle Summit, referred those plants to *Saxifraga ?eriophora* S. Watson.

Hultén (1967, 1968b) published *Saxifraga nivalis* var. *rufopilosa*, based on his collections from near Mastodon Dome, not far from Eagle Summit, noting the more or less "*dense rufo-pilosa*" of the under surface of the leaves and also its purple petals. He also wrote that his var. *rufopilosa* was the same as Porsild's *?eriophora.*

In 1974 Porsild compared var. *rufopilosa*, *M. tenuis*, and *M. nivalis,* referring to the specimens at CAN and those recently collected by his brother Robert along the Dempster Highway in the Yukon. He concluded that var. *rufopilosa* is more similar to *M tenuis* than to *M. nivalis*, but different from both at the rank of species, thus his combination *Saxifraga rufopilosa* (Hultén) A.E. Porsild.

Obviously, the inclusive taxonomy in which Scoggan (1978) subsumes *M. tenuis* and *M. gaspensis* within *M. nivalis,* is not followed by us.

HYBRID ORIGIN?

Morphological intermediacy is a typical feature of hybrids, and *M. rufopilosa* has been reported to be in some respects intermediate to *M. tenuis* and *M. nivalis*. The assumption of morphological intermediacy needs to be critically evaluated. After examining a number of specimens of all three species, we do not share it. Are there other reasons to assume hybrid origin? *Micranthes nivalis* and *M. tenuis* are well known to have chromosome numbers of $2n = 60$ and $2n = 20$ respectively, based on more than 20 independent countings.

Citing Krause and Beamish (1973), Gervais et al. (1995), and Devyatov et al. (1997), Healy and Gillespie (2004) pointed to the occurrences of $2n = 40$ plants on Wrangel Island in arctic Russia and in southwestern subarctic Yukon, where both *M. tenuis* ($2n = 20$) and *M. nivalis* ($2n = 60$) are found, and on the Gaspé as *M. gaspensis* ($2n = 40$) where neither putative parent is extant.

Brouillet and Elvander (2009) in their discussion of *Micranthes gaspensis* (Fernald) Small agreed with Gervais et al. (1995) that this species represents a stabilized F1 hybrid between *M. nivalis* and *M. tenuis*. They went on to infer that a count of $2n = 40$ from southwest Yukon published by Krause and Beamish (1973) was also the product of hybridization between *M. tenuis* and *M. nivalis*. The count was given as "*S. nivalis-tenuis* complex" by Krause and Beamish (1973), which we cannot check as the voucher specimen, despite a careful search by Bruce Bennett (pers. comm.) and by us, has not been found. As for *M. rufopilosa* there is no evidence of meiotic abnormalities, often a consequence of hybridization, inasmuch as plants readily form normal anthers (pollen stainability not determined), fruits, and seeds.

Whereas hybridization between *M. nivalis* and *M. tenuis* may be the correct explanation for the occurrence of *M. gaspensis*, further work is required to provide evidence. It is pure speculation to apply this possible origin also to the Alaska-Yukon *M. rufopilosa*. That there exists a chromosome count of $2n = 40$ in southwestern Yukon does not mean that *M. rufopilosa* has that number and, by extension, an origin through a *M. nivalis* x *M. tenuis* cross. Moreover, *M. rufopilosa* differs from *M. gaspensis* in important ways (see below). If the stabilized hybrid explanation is correct, then crosses by the same parents in different areas have produced very different results.

One must ask why, where both *M. tenuis* and *M. nivalis* are sympatric, sometimes growing in mixed stands, such as throughout the Scandinavian mountains and in the Svalbard Archipelago of arctic Norway, throughout northern Greenland and arctic Canada, and in most of arctic Russia, intermediates, fertile or sterile, have not been found and no counts of $2n = 40$ have been made except for the one from Wrangel Island. Hybridization, if that is the explanation for the existence of $2n = 40$ cytotypes, must be a very rare event.

TAXONOMY AND DESCRIPTIONS

Micranthes rufopilosa (Hultén) D.F. Murray & Elven

Plants 2–12 cm tall; stems 1–3(5) from short rootstock, stems and inflorescence with mixed long, multicellular white hairs *and* brown hairs; leaves with reddish-brown hairs along margins and petioles, typically densely matted on lower leaf surface; inflorescence initially a compact terminal cluster of short-pedicellate flowers, racemose to paniculate in fruit; flowers with pink to purple petals.

Micranthes nivalis (L.) Small, N. Amer. Fl. 22:136. 1905. *Saxifraga nivalis* L. Sp. Pl.:401. 1753. Type: Europe Herb. Linn 517.19 far right hand specimen (lectotype, designated by Jonsell & Jarvis 2002:72: LINN).

Plants 4–20 cm tall; stems 1–8 from a stout, simple or branched rootstock; stems and inflorescence with long, multicellular, white to clear hairs, some purple-tipped; leaves glabrous or with reddish-brown hairs on margins of blades and petioles, sometimes densely covering lower leaf surface; inflorescence initially one or more compact terminal clusters of flowers, , racemose, in fruit; flowers with white petals turning pink with age.

Micranthes tenuis (Wahlenb.) Small. N. Am. Fl. 22:136. 1905.

Saxifraga tenuis (Wahlenb.) Harry Sm. ex Lindm.

Saxifraga nivalis var. *tenuis* Wahlenb. Fl. Lapp.:114. 1812 Type: Sweden. Kajsats, 30 Jul 1807, leg. G. Wahlenberg (lectotype, designated by Moberg & Nilsson 1991:294: UPS!)

Plants 1–10 cm tall; stems 1–6(10) from a stout rootstock, stems glabrate below with short, multicelular, crisp white hairs above, sometimes densely so, mixed with short glandular hairs; cell walls violet or purple; leaves glabrous or with reddish-brown hairs along margins of blades and petioles, sometimes densely covering lower leaf surface; inflorescence a compact terminal cluster in flower becoming corymbose in fruit; flowers with pink to purple petals, exceptionally white.

Micranthes gaspensis (Fernald) Small. N. Amer. Fl. 22:552. 1918.

Saxifraga gaspensis Fernald. Rhodora 19:141–142. 1917. Type: CANADA. Québec: Gaspé, Tabletopped Mt., Alt. 1000–1100 m, 8 & 12 Aug 1906, *Fernald & Collins 600* (holotype: GH digital image!; isotype: CAN!).

Saxifraga nivalis var. *gaspensis* (Fernald) B. Boivin

Plants 3.5–10 cm tall; stems 1–2(5) from a stout rootstock, stems and inflorescence pubescent with short white hairs, glabrate below gradually more densely pubescent above, some hairs glandular-tipped; leaves glabrous or margins ciliate, with tangled reddish-brown hairs on lower leaf surface; inflorescence a compact terminal cluster of flowers becoming racemose in fruit; flowers with white petals.

Porsild (1974) provided photos (plates 8 and 9) and a brief, useful review of diagnostic features that distinguish *M. rufopilosa* from *M. tenuis* and *M. nivalis*. *Micranthes rufopilosa* takes its name from the dense layer of reddish-brown hairs on the lower surface of some leaves; however, the leaves are not consistently so. Moreover, *Micranthes tenuis*, *M. nivalis*, and *M. gaspensis* also have reddish-brown hairs on the petiole and leaf margins and in some instances also on the lower surface of the leaves, although only occasionally as dense as in *M. rufopilosa*.

On stems and branches of the inflorescence *M. rufopilosa* has mixed long, white and reddish-brown hairs, similar in length to the long white, crisp hairs of *M. nivalis*. *Micranthes nivalis* has only long white hairs, *M. gaspensis* has short white hairs, and *M. tenuis* is typically sparsely short-hairy, more dense distally, with a mixture of short, glandular hairs.

Specimens of *Micranthes rufopilosa* we have seen are all from the Yukon-Tanana Upland of central Alaska and from central and southern Yukon. Cody (1996) has mapped arctic localities well disjunct of its main range in Yukon; these arctic occurrences have been determined by us as *M. tenuis*.

KEY TO SPECIES

1. Petals white or margins pink with age; stems glabrous or with only white hairs, hypanthium triangular to hemispheric.
    2. Stems and inflorescence with *short crisp and long* tangled white hairs ______ **M. nivalis**
    2. Stems and inflorescence glabrate or with short white hairs ______ **M. gaspensis**
1. Petals reddish to purple; stems pubescent not as above, hypanthium turbinate.
    3. Stems with *long tangled white and brown hairs;* inflorescence racemose or paniclate in fruit ______ **M. rufopilosa**
    3. Stems glabrate or with *short white and short, glandular hairs;* inflorescence corymbose in fruit ______ **M. tenuis**

Representative specimens (*Micranthes rufopilosa*).—**U.S.A. ALASKA. Charley River Quad.:** Mt. Sorenson, 65°00'N, 142°45'W, 19 Jul 2002, *Cook & Roland 02-443* (ALA). **Circle Quad.:** Steese Hwy. Eagle Summit, 26 Jul 1964, *Viereck 7397* (ALA) [collected at the same time and place as the type was gathered by Eric Hultén]. **Nabesna Quad.:** Chisana R., 62°16'N, 141°55'W, 20 Jun 2003, *Roland & Batten 5817B* (ALA). **Livengood Quad.:** White Mts., Vic. VABM Fossil, 65°37'N, 147°22'W, 13 Jun 1995, *Parker & Herriges 5639* (ALA). **CANADA. Yukon:** Klaza Mt. 62°27'N, 137°51'W, 19 Jul 2012, *Bennett & Cannings 12-0243* (ALA). Syenite Range, 63°95'N, 137°27'W, 26 Jun 2012, *Bennett, Cannings, & Schroeder 12-0064* (ALA); Mt. Klotz, 65°37'N, 140°17'W, 24 Jun 2007, *Bennett, Line, Kennedy, & Mennell 07-118* (ALA); Ptarmigan Heart, 61°49'N, 138°35'W, 16 Jul 1948, *Raup, Drury, & Raup, 13749* (CAN); Ogilvie Mts., Dempster Hwy. Mile 51, 7 Jul 1968, *Porsild 1574* (CAN) [basis for photo in A.E. Porsild 1974.]; Mt. Nansen, 62°06'N, 137°17'W, 16–17 Jun 1968, *Porsild 1372* (CAN); Mt. Archibald, Mile 1026 Alaska Hwy., 23 Jul 1967, *Pearson 67-297A* (CAN); Dawson Range, 62°35'N, 138°20'W, 27 Jun 1941, *Bostock 256* (CAN).

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NRDNA SEQUENCE (ITS AND ETS) FROM HERBARIUM SPECIMENS REVEALS PHYLOGENETIC AFFINITIES OF *ERIGERON GEISERI* (ASTERACEAE)

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ABSTRACT

Erigeron geiseri Shinners is a tap-rooted herbaceous daisy occurring from south-eastern Texas to southern Oklahoma. Our study of pollen quality from 67 herbarium specimens supports the hypothesis that the species comprises sexual diploid populations, restricted to southern locations, and polyploid, putatively apomictic, populations that are widespread. We successfully amplified and sequenced ITS and ETS spacer regions of nrDNA for five specimens (two putative sexual diploids, three putative apomictic polyploids). Phylogenetic analysis conducted using maximum likelihood and Bayesian methods support a topology showing that 1) sexual and apomictic populations of *E. geiseri* form a well-supported monophyletic group, and, 2) *E. geiseri* is sister to *E. strigosus* of eastern North America. The results support the classification of *E. geiseri* with *E. strigosus* in *E.* sect. *Phalacroloma*.

RESUMEN

Erigeron geiseri Shinners es una margarita herbácea que se da desde el sureste de Texas al sur de Oklahoma. Nuestro estudio de la calidad del polen en 67 especímenes de herbario soporta la hipótesis de que especie comprende poblaciones sexuales diploides, restringidas a localidades sureñas, y poblaciones poliploides, putativamente apomícticas, que están esparcidas. Amplificamos y secuenciamos con éxito las regiones de los espaciadores ITS y ETS del nrDNA de cinco especímenes (dos diploides sexuales putativos, tres poliploides apomícticos putativos). Los análisis filogenéticos realizados usando máxima verosimilitud y métodos Bayesianos soportan una topología que muestra 1) las poblaciones sexuales y apomícticas de *E. geiseri* forman un grupo monofilético bien soportado, y, 2) *E. geiseri* is es hermano de *E. strigosus* del este de Norte América. Los resultados soportan la clasificación de *E. geiseri* con *E. strigosus* en *E.* sect. *Phalacroloma*.

INTRODUCTION

Erigeron geiseri Shinners (Asteraceae), Geiser's fleabane or Basin fleabane, was originally described (Shinners 1947) from collections within a few-county radius around Austin in central Texas (Burnet, Bastrop, Falls, Guadalupe, Llano, and Robertson counties). Subsequent study documented the range of the species from the south-eastern coast of Texas north to southern Oklahoma (Nesom 1979). Although the global conservation status of G4 for *E. geiseri* indicates it is apparently secure (NatureServe 2014), most of its relevant biological or ecological attributes have not been assessed. Further, the taxon is ranked S3 for Texas (vulnerable), and either not ranked or under review for Oklahoma. The species (Fig. 1) is a tap-rooted annual to 40 cm with narrow oblanceolate leaves, the basal ones often exhibiting 2-4 pair of conspicuous lobes. The inflorescence is a diffuse corymbiform array with 1-20 capitula, with peduncles often slightly dilated distally. The capitula feature obovate phyllaries with scarious margins, and low-conic receptacles. Ray florets in the species are white, the relatively few disc flowers are yellow, and cypselae bear a biseriate pappus consisting of about 10 scabrous bristles and an equal number of low scales (Nesom 2006). The species flowers from late March–May (–June) and is distributed with broad ecological tolerance, occurring on sandy to clay soils associated with prairie, roadside, and fencerow habitats. Upon publishing *E. geiseri*, Shinners also described the intraspecific taxon *E. geiseri* var. *calcicola* Shinners for plants with longer stem pubescence and a pappus reduced to a low crown. These plants have subsequently been synonymized with *E. versicolor* (Greenm.) Nesom (Nesom 2006).

While a chromosome number for *E. geiseri* has not been published, specimen annotations by Dr. B.L. Turner, University of Texas, indicate $2n=18$ (Turner #4526, TEX), the typical number for diploid *Erigeron*, as well as triploids with $2n=27$ (Turner #4527, TEX). The unpublished numbers intimate that *E. geiseri*, similar to

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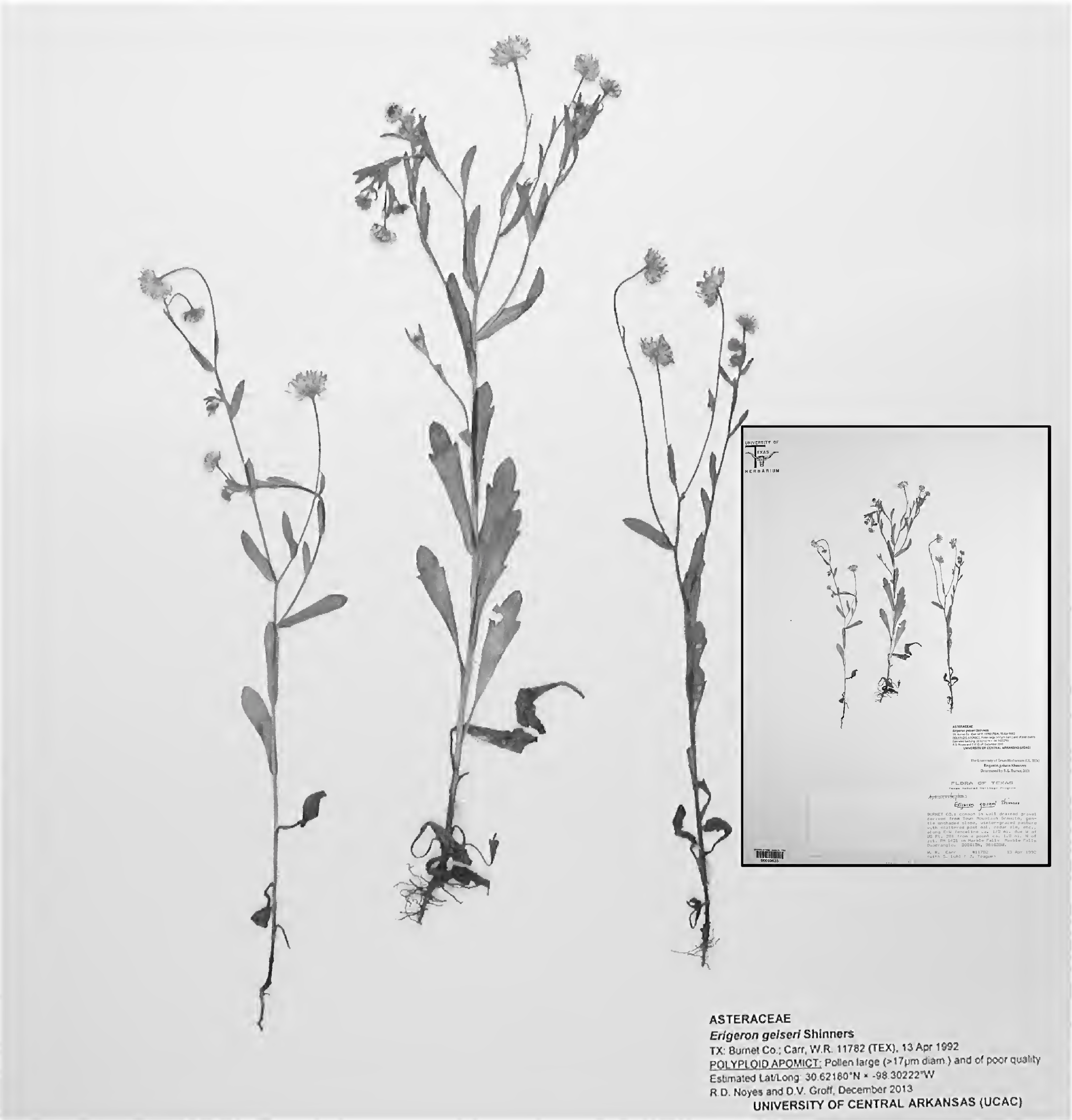
ASTERACEAE
Erigeron geiseri Shinners
TX: Burnet Co.; Carr, W.R. 11782 (TEX), 13 Apr 1992
POLYPLOID APOMICT: Pollen large (>17μm diam.) and of poor quality
Estimated Lat/Long: 30.62180°N × -98.30222°W
R.D. Noyes and D.V. Groff, December 2013
UNIVERSITY OF CENTRAL ARKANSAS (UCAC)

Fig. 1. Herbarium specimen of *Erigeron geiseri*. Carr 11782 (TEX) exhibits the tap-root, small stature, erect habit, diffuse inflorescence, and occasional leaf lobing that characterize the species. The largest specimen in the center, including the root, is 20.3 cm tall. Inset shows the entire herbarium specimen.

congeners such as *E. strigosus* and *E. tenuis*, likely comprises diploid, presumably sexual populations, and triploid populations that likely reproduce via apomixis (Noyes 2006; Groff 2010; Noyes & Givens 2013).

Differing hypotheses regarding the taxonomic affinities of *Erigeron geiseri* have been proposed. Shinners (1947) allied *E. geiseri* with the Mexican taxon *E. coronarius* Greene, presently classified within *E.* sect. *Geniculactis* (Nesom 2008). Nesom (1989) placed *E. geiseri* within a broadly defined *E.* section *Olygotrichium*, calling attention to morphological similarities among *E. geiseri*, *E. tenuis* Torr. & A. Gray, *E. tenellus* DC., and *E. turnerorum* Nesom. Nesom (2008) later included *E. geiseri* within the segregate *E.* sect. *Quercifolium*, along with 18 other species including *E. tenellus* and *E. turnerorum*. Morphological similarity between *E. geiseri* and *E. tenuis* (Shinners 1947; Nesom 1979; Nesom 1989; Nesom 2008) adds an additional twist as *E. tenuis* has been shown to be genetically similar to *E. strigosus* Muhl. ex Willd. and *E. annuus* (L.) Pers. of eastern North America (Noyes 2000; Groff 2010) all presently classified as *E.* sect. *Phalacroloma* (Nesom 2008).

The objective of this study was to utilize herbarium specimens 1) to estimate, from study of pollen quality, the distribution of putative sexual diploid and apomictic polyploid populations of *Erigeron geiseri*, and, 2) to evaluate the phylogenetic affinities of *E. geiseri* using nuclear ribosomal DNA spacer sequence data (ITS and ETS). Results provide data relevant to the conservation of *E. geiseri* and help to clarify our understanding of the relationships among the *Erigeron* species of eastern North America.

METHODS

Mode of reproduction and geographic mapping

A total of 67 herbarium specimens of *Erigeron geiseri* were studied. The majority were obtained on loan from the University of Texas (TEX & LL; 44 specimens) and from the Botanical Research Institute of Texas (BRIT; 18 specimens). Five specimens were also studied that were originally misidentified and included among loans for the study of other *Erigeron* species (Missouri Botanical Garden, MO, 4 specimens; Mississippi State University, MISSA, 1 specimen).

Pollen from the 67 herbarium specimens was evaluated to estimate mode of reproduction (Noyes & Allison 2005; Noyes & Groff 2011). Samples from mature but unopened florets were stained in Cotton Blue in lactophenol (Stanley & Linskens 1974) for a minimum of four days and evaluated at 400X on an Olympus BX51 compound microscope using bright field optics. A pollen sample was interpreted to represent the sexual diploid condition if the grains were uniformly small (12–15 µm diam.) with a high percentage darkly stained, putatively viable, grains (Noyes & Allison 2005). The polyploid apomictic condition, by contrast, was indicated by samples that included large grains (>17 µm diam.), high proportion of non-staining aborted grains, and frequent non-staining pollen micrograins. Sample measurements of grains were performed using AnalySIS (v. 3.1; soft Imaging System, GmbH) on images captured with an Olympus FV12 monochrome CCD camera.

For distribution mapping, the geographic coordinates for each specimen were estimated from label locality information using TOPO USA (version 5.0, DeLorme, Yarmouth, ME). The data were then plotted using ESRI ArcInfo (v. 9.2, copyright 2004-2007; http://www.esri.com). The base map providing a county boundary layer (tl_2009_US_county.shp) was obtained from the US Census Bureau, Geographic Products Branch (http://www2.census.gov/cgi-bin/shapefiles2009/national-files). Records from duplicate specimens were culled so that only unique collections were mapped. As a rough check of the accuracy of our plotted data, we verified that county names extracted from plotted data points matched input county names. Annotation labels were affixed to all specimens indicating putative mode of reproduction and estimated geographic coordinates.

DNA isolation, amplification, and sequencing

To investigate the genetic relationships of *E. geiseri,* we selected eight relatively recently collected specimens (four putative sexual diploid, four putative polyploid apomicts) with ample leaf material (Table 1). Total DNA was isolated for each specimen using the DNeasy Plant Mini kit (#69106, QIAGEN Inc., Valencia, CA, USA) using about 0.5 cm^2 dried leaf tissue. The prescribed protocol was followed except that to 500 µl warmed AP1 within a 1.6 ml Eppendorf tube we added a small quantity of sterilized sand to facilitate grinding, plus 10mM sodium metabisulfite (#S244, Fisher Scientific, Pittsburgh, PA, USA) as a supplemental antioxidant (Horne et al. 2004). In addition, we heated the grindate in AP1 for 0.5 hour, and employed a 13K centrifugation for 5 min. after incubation with AP2 prior to application to the shredder column to facilitate removal of protein precipitate and undigested leaf tissue. Samples were eluted into a total of 60 µl AE (rather than the recommended 200 µl) to foster higher yield concentrations. The resulting genomic DNA was quantified via fluorometry (Hoefer DyNA Quant 200, Amersham Biosciences, Piscataway, NJ, USA) and evaluated for quality by agarose electrophoresis. Samples exhibiting at least a portion of genomic DNA greater than 1kb in size were selected for sequence analysis.

We sequenced the 18S-26S nrDNA spacer regions ITS (ITS1, 5.8S, ITS2) and ETS to facilitate comparisons

Table 1. Herbarium specimens of *Erigeron geiseri* selected for DNA study.

Specimen	Designation	Isolated DNA Suitable for Sequence Analysis?	GenBank Accession Numbers
	Putative sexual diploids		
1. *Fleetwood, R. J. 9049* (TEX); Texas: Brazoria Co., 13 April 1967.	S1	NO	
2. *Fleetwood, R. J. 10811* (LL); Texas: Galveston Co., 04 March 1974.	S2	NO	
3. *Lieb, C. S. 337* (TEX); Texas: Matagorda Co., 09 April 1983.	S3	YES[1]	ITS: KP318874 ETS: KP318879
4. *Nesom, G.L. 5389* (TEX); Texas: Gonzales Co., 27 March 1986.	S4	YES	ITS: KP318875 ETS: KP318880
	Putative apomictic polyploids		
1. *Carr, W. R. 11782* (TEX); Texas: Burnet Co., 13 April 1992.	A1	YES	ITS: KP318876 ETS: KP318881
2. *Carr, W. R. 23324* (TEX); Texas: Goliad Co., 27 May 2004.	A2	YES	ITS: KP318877 ETS: KP318882
3. *Smith, B. 17* (BRIT); Texas: McCollough Co., 06 April 1966.	A3	NO	
4. *Turner, B. L. 4527* (TEX); Texas: Gonzales Co., 27 March 1959.	A4	YES[1]	ITS: KP318878 ETS: KP318883

[1] Required internal amplification for ITS and ETS from initial weak PCR products.

with other *Erigeron* species (Noyes 2000; Noyes 2006). ITS and ETS were amplified and sequenced separately using a modification of the PCR conditions of Urbatsch et al. (2003). The program we used (for both ITS and ETS) consisted of a 3-min 95°C initial denaturation followed by 10 cycles of 30-sec denaturation at 95°C, 40-sec annealing at 55°C, and 40-sec extension at 72°C with a 4-sec per cycle increase. The subsequent 20 cycles proceeded with 30-sec denaturation at 95°C, 40-sec annealing at 50°C, and 40-sec extension at 72°C (with 4-sec per cycle increase), followed by a final extension of 7-min at 72°C. We employed relatively simple PCR components including (in ~50 ul reactions) 41.3 µl PCR grade H_2O, 5 µl 10× ThermoPol Reaction Buffer (New England Biolabs, Beverly, MA, USA), 0.2 µmol/L each primer (1.0 µl of 10uM stock), 200 µmol/L each dNTP (0.4 µl of mixture of 25 mmol/L each dNTP; #N0446S, New England Biolabs), 1.5 U (0.3 µl) ThermoPol Taq polymerase (#M0267X, 5,000U/ml, New England Biolabs), and 0.5 to 2.0 µl of undiluted genomic DNA (ranging from 2 to 44 ng/µl).

We successfully amplified and sequenced ITS and ETS for five of the eight samples using a suite of internal and external primers (Table 2; Fig. 2). The ITS region was amplified using primers ITSI(f) and ITS4(r) while ETS was amplified using ETS-Ast8(f) and ETS-18S(r). For three samples that yielded strong amplifications for both regions, PCR products were purified for sequencing using MinElute PCR purification columns (#28006, QIAGEN Inc.). Products were eluted in a final volume of 18 µl, quantified by fluorometry, and sequenced using separate forward and reverse reactions. For the ITS region, the primer ITS5 was used for the forward sequence and ITS4 was used for the reverse sequence. For the ETS region, PCR primers (ETS-Ast8 and ETS-18S) were used for sequencing.

Two samples yielded faint initial ITS and ETS PCR bands. For these we increased yields by internal amplification using 1 µl of undiluted initial PCR product as a template using identical cycling conditions as described above. For the ITS1 region we used primers ITSI(f) and ITS2(r) while for the ITS2 region we used primers ITS3(f) and ITS4(r). For internal amplification of ETS we identified a centrally located conserved

Table 2. Primers used in this study to amplify ITS and ETS 18S-26S nrDNA spacer regions.

Primer Designation	Primer Sequence	Reference
ETS		
ETS-Ast8(f)	TTC TCT TCG TAT CGT GCG GT	Markos & Baldwin (2001)
ETS-18S(r)	ACT TAC ACA TGC ATG GGT TAA TCT	Baldwin & Markos (1998)
ETS-iR(r)	GAG TGT GTT GCA TGG TTC	This study
ETS-iF(f)	GAA CCA TGC AAC ACA CTC	This study
ITS		
ITSI(f)	GTC-CAC-TGA-ACC-TTA-TCA-TTT-AG	Urbatsch et al. (2000)
ITS5(f)	GGA-AGG-AGA-AGT-CGT-AAC-AAG-G	White et al. (1990)
ITS4(r)	TCC-TCC-GCT-TAT-TGA-TAT-GC	White et al. (1990)
ITS2(r)	GCT-ACG-TTC-TTC-ATC-GAT-GC	White et al. (1990)
ITS3(f)	GCA-TCG-ATG-AAG-AAC-GTA-GC	White et al. (1990)

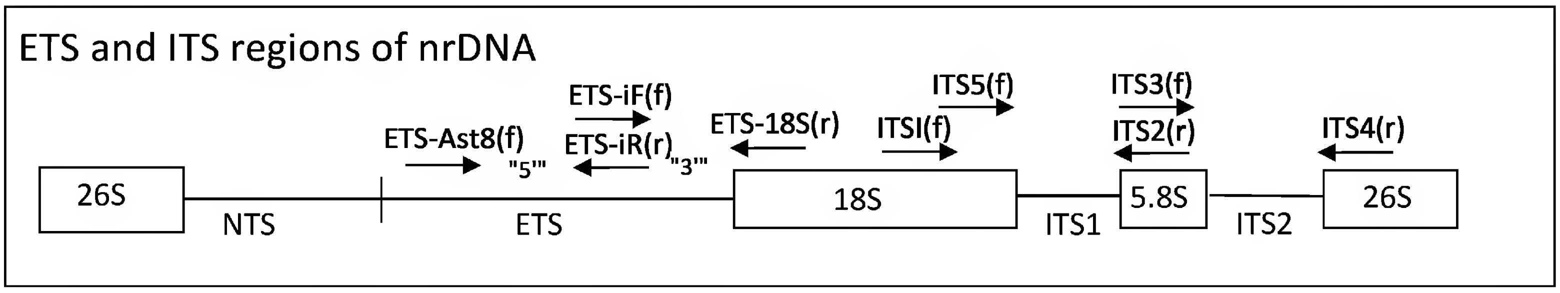

Fig. 2. Approximate locations of primers used to amplify the ITS and ETS 18S-26S nrDNA spacer regions in this study.

sequence among a diverse sample of *Erigeron* taxa (Noyes, 2006) and designed internal forward and reverse primers (Table 2). Internal amplification of the 5'ETS region thereby employed primers ETS-Ast8(f) and ETS-iR(r) and the 3'ETS region employed primers ETS-iF(f) and ETS-18s(r). PCR products were purified and quantified as above. Sequencing of the ITS1 fragment employed, separately, ITS5 and ITS2 primers. Sequencing of the other three products (ITS2, 5'ETS, 3'ETS) employed the primers used for internal PCR.

Samples for sequencing consisted of 150 ng purified PCR product plus 10 pmol (1 µl x 10 µM stock) sequencing primer. Samples were dried using an Eppendorf Speedvac for 20 min at 65°C and shipped via First Class USPS to the University of Missouri, Columbia, DNA Core Facility, which employs an Applied Biosystems (Foster City, CA, USA) 3730xl 96-capillary DNA Analyzer and Big Dye Terminator cycle sequencing chemistry. Forward and reverse chromatograms, downloaded by FTP, were merged into contigs and edited using Sequencher 4.2 (Gene Codes Corp., Ann Arbor, MI, USA). Care was taken to score bases as polymorphic when there were obvious double peaks in both forward and reverse sequences.

Phylogenetic analyses

Analysis was first conducted using 81 ITS sequences to broadly evaluate the relationship of *Erigeron geiseri* to other *Erigeron* species (Appendix 1). The data matrix included five sequences for *E. geiseri*, 75 published ITS sequences for Astereae sect. Conyzinae (*Erigeron* and allies; Noyes 2000), plus the ITS sequence for *E. hyssopifolius* Michx. (Noyes 2006). In addition, we substituted three sequences from the Noyes (2000) matrix representing *E.* sect. *Phalacroloma* (*E. strigosus* (GenBank #AF118490), *E. annuus* (AF118489), and *E. tenuis* (AF118488)), with those published for *E. strigosus* var. *calcicola* J. Allison (AY871318), *E. strigosus* var. *dolomiticola* J. Allison (AY871323), and *E. strigosus* var. *strigosus* (AY871333) that study showed better represented genetic diversity in the group (Noyes 2006). *Erigeron neomexicanus* A. Gray (AF118544) served as the Outgroup.

Initial results indicated that further analysis with more comprehensive representation of *Erigeron* sect. *Phalacroloma* was warranted. We therefore conducted a second analysis with concatenated ITS and ETS sequences for a representative sample of 14 sequences for *E.* sect *Phalacroloma*, the five sequences obtained here for *E. geiseri*, plus five additional *Erigeron* for which both ITS and ETS were available (Noyes 2006; Appendix 2). The 14 sequences for *E.* sect. *Phalacroloma* include those for *E. strigosus* var. *calcicola*, *E. strigosus* var. *dolomiticola*, plus 12 sequences representing the three divergent rDNA haplotypes (I, II, III) found for sexual diploid *E. strigosus* var. *strigosus* (Noyes 2006). Sequences for *E. acris* L., *E. hyssopifolius*, *E. pinnatisectus* (A. Gray) A. Nelson, and *E. speciosus* (Lindl.) DC. served as the Outgroup.

Sequences for analyses were compiled and aligned using ClustalW as implemented in MEGA6 (Tamura et al. 2013). Genetic distances between subsets of sequences were explored in MEGA6 and phylogenetic analysis was conducted using Maximum Likelihood and Bayesian approaches. MrModelTest (2.3) (Nylander 2004) was employed to select appropriate models of sequence evolution. This was accomplished by exporting respective Nexus files (ITS vs. ITS plus ETS matrices) from MEGA6, appending the MrModelTest command block, and then implementing PAUP* (version 4.0b.10; Swofford 2002). This yielded ".scores" files that were employed by the MrModelTest executable to produce a ".out" file containing test scores and recommended command lines to implement the optimal model of molecular evolution (based on the Akaike Information Criterion (AIC)) for phylogenetic analysis.

Maximum likelihood analyses were executed in MEGA6 using the nearest-neighbor-interchange (NNI) heuristic method with the initial tree generated automatically by neighbor joining. Analyses used the default settings of "branch swap filter = very strong", and "number of threads = 1". Gaps and missing data were subject to complete deletion and analyses were run with 500 bootstrap replicates. Bayesian analyses were implemented with MrBayes 3 (Ronquist & Huelsenbeck 2003) by appending the prescribed commands from MrModelTest to the respective Nexus files. The program was executed using the Markov chain Monte Carlo (MCMC) method with four chains, 3 million generations, print frequency of 1000, sample frequency of 100, and with branch lengths saved. The number of initial trees discarded ('burnin') was determined by visually approximating the point at which the average standard deviation of split frequencies appeared to stabilize. Bayesian probabilities for nodes were obtained from the resulting 50% compatibility consensus tree. Tree topologies summarizing analyses were those obtained from MEGA6 maximum likelihood analyses, to which maximum likelihood and Bayesian probabilities were added. Topologies, as necessary, were edited with TreeView 1.6.6 (Page 1996).

RESULTS

All 67 specimens of *Erigeron geiseri* yielded pollen from which we were able to unequivocally classify mode of reproduction. A total of 61 of the collections were unique; six duplicates were identified. A total of 12 (19.7%) of the unique collections yielded pollen consistent with the sexual diploid condition and 49 (80.3%) produced pollen characteristic of apomicts (Fig. 3). All duplicates of a collection exhibited the same pollen characteristics and therefore no duplicate sets provided evidence that populations included both sexual and apomictic plants. The putative sexual diploid populations occur in two geographically adjacent but distinct areas (Fig. 4). The first group (six collections) occurs along the Gulf Coast in Texas from Galveston Co. south to San Patricio Co. The second group (also six collections) is approximately 200 km inland scattered across five counties in Texas in the vicinity of Austin. Putative apomictic *E. geiseri* is sympatric with but more broadly distributed than sexual populations with collections extending from Kleberg Co., along the southern Gulf Coast, north to south-central Oklahoma, and west in Texas to Shackelford, Callahan, and McCulloch Cos. Reflecting the difference in distribution, the mean latitude for apomicts (30.785°N) is significantly (one-tailed t-test, $P = 0.0049$) more northerly than that for sexual diploids (29.253°N). The overall map is nearly identical to that of Nesom (1978), but with the added reproductive data.

The map indicates the strong possibility of co-occurrence of the two reproductive modes because four of the ten counties where sexual collections are recorded also exhibit apomictic collections. In addition, collection dates, as a proxy for flowering time, document that putative sexual diploid and apomictic polyploid populations flower at similar times (from mid-March to early June) intimating the possibility for gene flow between

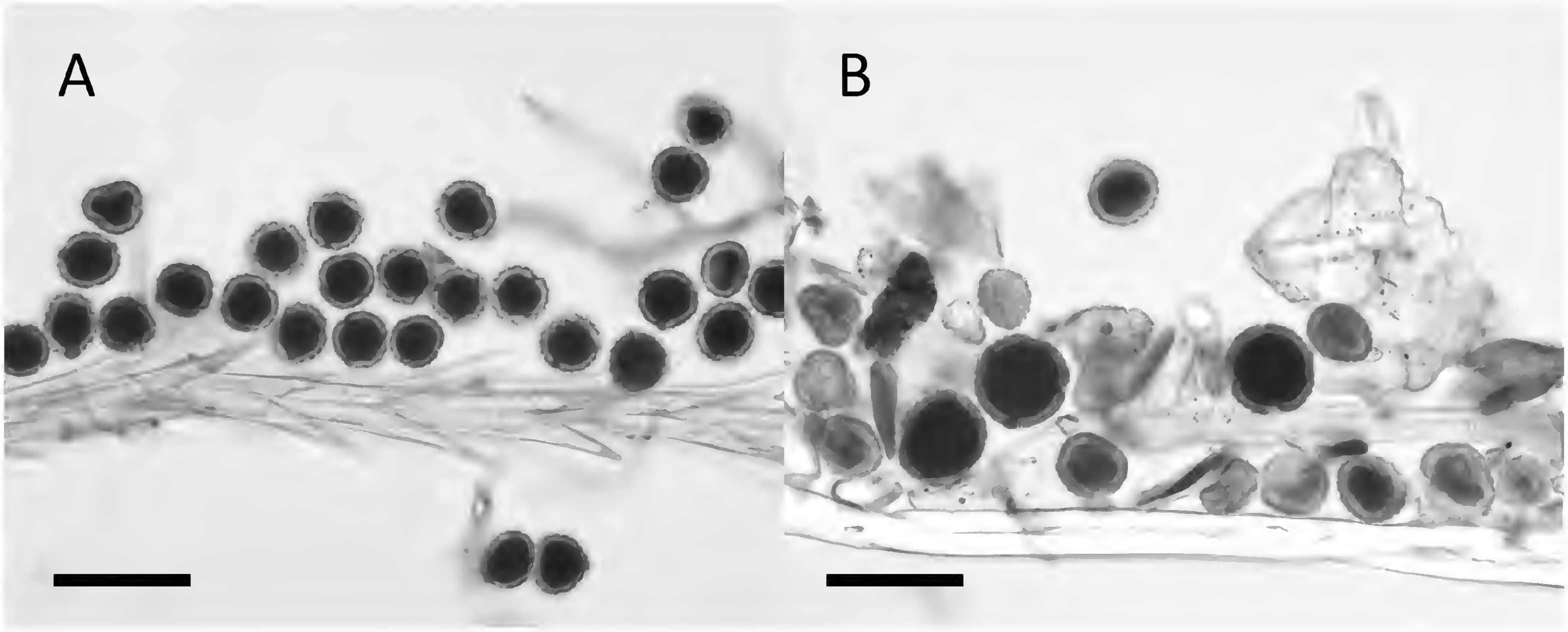

Fig. 3. Pollen of herbarium specimens of *Erigeron geiseri* stained in cotton blue in lactophenol. A. Pollen for Fleetwood #9049 (TEX) shows small grains (~15 µm diameter) with a high proportion staining darkly consistent with plants of the sexual diploid condition. B. Pollen for Tharp #7448 (TEX) shows a mixture of staining grains that vary in size, plus a high proportion of grains that are unstained or lightly stained, consistent with the polyploid apomictic condition. The largest staining grains are ~21 µm diameter and possibly triploid. Scale bar = 40 µm.

the two types. The overall average date of collection for apomictic plants is significantly later than for sexual plants (30 April vs. 14 April; one-tailed t-test, P = 0.026), but this is likely a consequence of the more northerly range of apomictic plants. When 29 apomictic plants are excluded that occur further north than the northernmost sexual collection, the mean flowering date for putative apomicts shifts to 25 April and the difference between sexuals and apomicts is not significantly different (one-tailed t-test, P = 0.11).

We obtained ITS and ETS sequences for five of the eight assayed herbarium specimens, including two putative sexual diploids ('S3' and 'S4') and three putative apomicts ('A1', 'A2', and 'A4'). Successful sequencing of 'S3' and 'A4' required second amplification from weak initial PCR products using internal primers. GenBank numbers are provided in Table 1. The sequenced specimens represent well the geographic distribution of *E. geiseri*, with 'S3' and 'S4' representing coastal and interior sexual diploid populations, respectively, and 'A1', 'A2', and 'A4' well separated by latitude across the range of apomicts. Extracts from 'S1', 'S2', and 'A3' did not exhibit high molecular weight DNA and did not yield visible ITS or ETS PCR products.

The length of the ITS and ETS sequences were consistent with those for other *Erigeron* and allies within sect. Conyzinae: 625-626 bp for ITS and 597 bp for ETS. The total number of polymorphisms per concatenated sequence ranged from 3 for 'S3' to 8 for 'A2', with an overall average of 5. Of these, 30% occurred at potentially informative sites, while 70% were unique and therefore not informative. Three of the sequences exhibited indel polymorphisms, which meant that complete sequence could be obtained only by reading a partial sequence from the forward read (to the polymorphic site) and the remaining sequence from the reverse read (to the polymorphic site). Single indel polymorphisms were inferred for 'A4' in ETS, and for 'S3' in ITS2. Two indels were detected in ETS for 'S3', one in the 5' and one in the 3' regions; these were resolvable because the region was sequenced in two separate fragments. The nucleotide and indel polymorphisms did not preclude acquisition of complete and robust nrDNA sequence. Overall the five sequences are very similar, differing by an average of only 0.08%, which corresponds to approximately a single base position (0.98) across the entire ITS plus ETS region.

The analysis of ITS for 76 members of *Erigeron* sect. *Phalacroloma* plus five *Erigeron geiseri* employed a general time reversible (GTR) model of molecular evolution with proportion of invariable sites (I) and gamma distribution of rate variation among sites (G). A partial topology showing the relationships of *E. geiseri* received high level of support for several key nodes (Fig. 5). The five sequences for *E. geiseri* form a clade with 0.99 Bayesian probability, though demonstrating little internal structure. *Erigeron geiseri*, in turn, forms a clade with *E.* sect *Phalacroloma* supported by 1.0 Bayesian probability and 98% bootstrap support from maximum

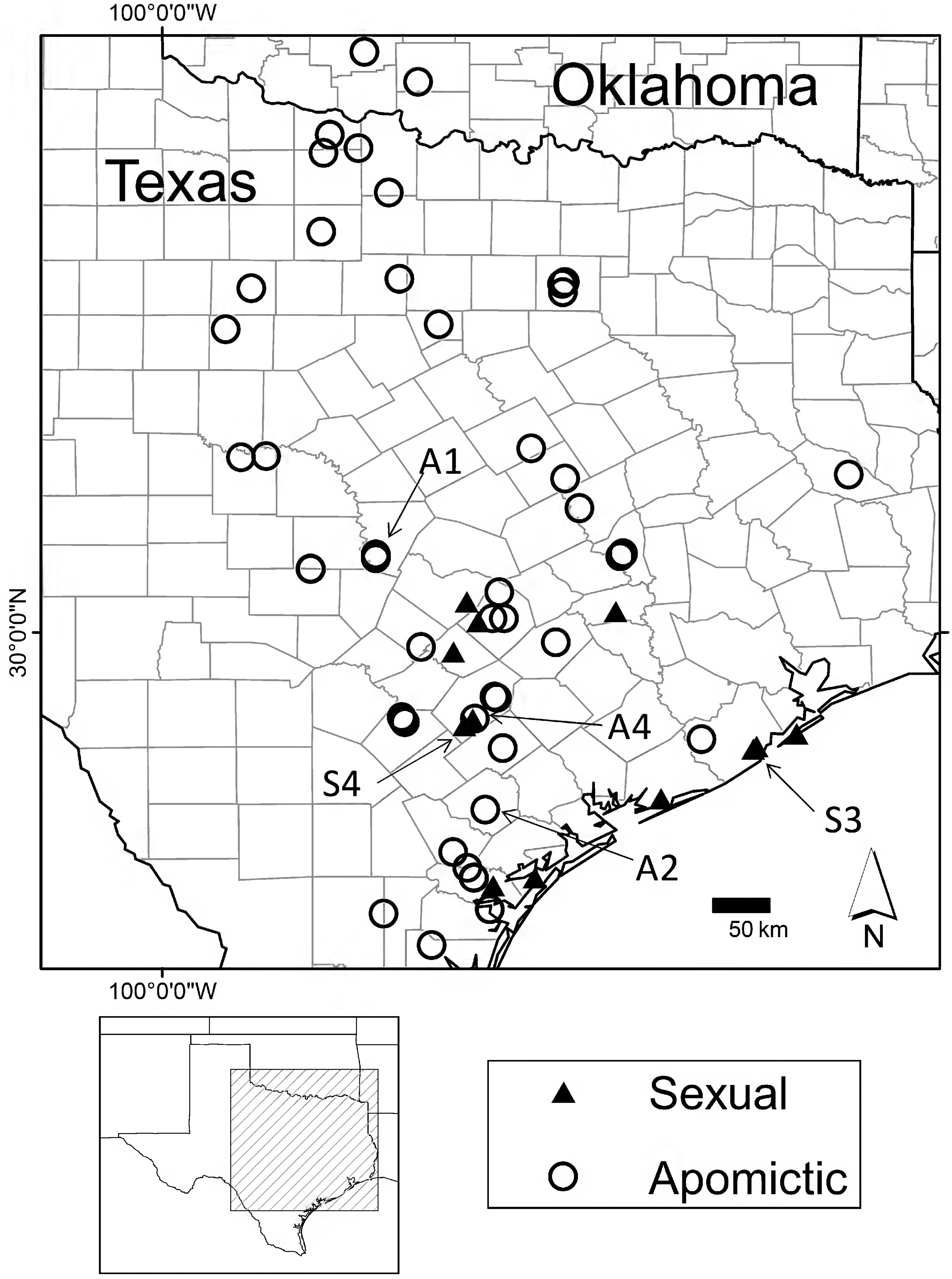
100°0'0"W
Oklahoma
Texas
A1
A4
S4
S3
A2
30°0'0"N
30°0'0"N
50 km
N
100°0'0"W
▲ Sexual
○ Apomictic

Fig. 4. Estimated geographic distribution of putative sexual diploid and polyploid apomictic *Erigeron geiseri* in Texas and Oklahoma, USA. 'S1-S4' and 'A1-A4' designate localities of specimens sampled for DNA study (Table 1).

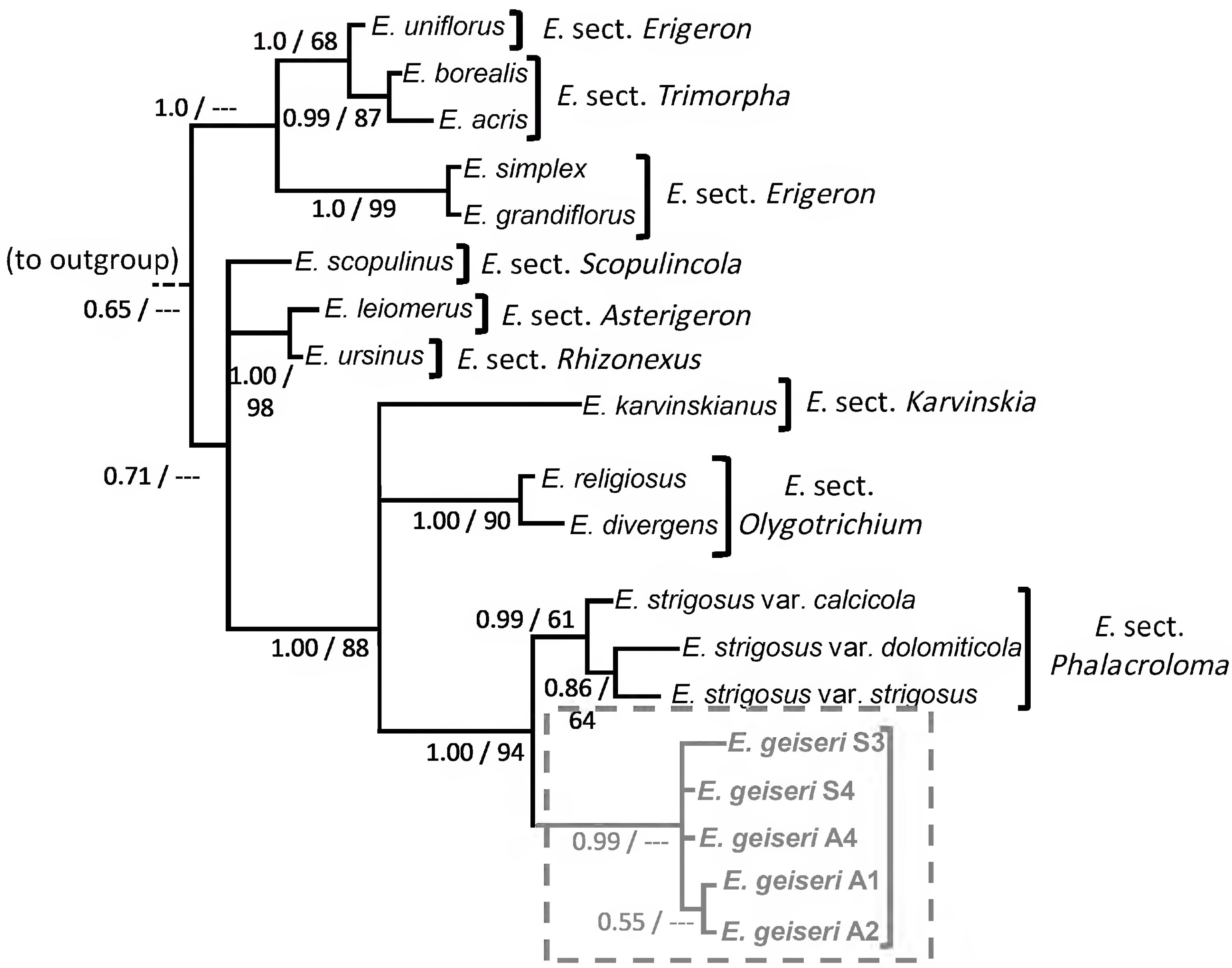
1.0 / 68
E. uniflorus
E. sect. Erigeron
E. borealis
E. sect. Trimorpha
1.0 / ---
0.99 / 87
E. acris
E. simplex
E. sect. Erigeron
1.0 / 99
E. grandiflorus
(to outgroup)
E. scopulinus
E. sect. Scopulincola
0.65 / ---
E. leiomerus
E. sect. Asterigeron
E. ursinus
E. sect. Rhizonexus
1.00 / 98
E. karvinskianus
E. sect. Karvinskia
0.71 / ---
E. religiosus
E. sect. Olygotrichium
1.00 / 90
E. divergens
E. strigosus var. calcicola
0.99 / 61
E. sect. Phalacroloma
1.00 / 88
E. strigosus var. dolomiticola
0.86 / 64
E. strigosus var. strigosus
E. geiseri S3
1.00 / 94
E. geiseri S4
0.99 / ---
E. geiseri A4
E. geiseri A1
0.55 / ---
E. geiseri A2

Fig. 5. Portion of ITS phylogeny for Astereae sect. Conyzineae. Sample designations for *E. geiseri* according to Table 1. Values at nodes are Bayesian probabilities and bootstrap percentages respectively. Phylogeny for 81 sequences (Appendix 1) generated using a GTR+I+G evolutionary model. Taxonomic sections according to Nesom (2008).

likelihood analysis. Together, *E.* sect. *Phalacroloma* and *E. geiseri* are sister to *E. divergens* Torr. & A. Gray and *E. religious* Cronquist (*E.* sect. *Olygotrichium*). *Erigeron* sect. *Phalacroloma*, *E. geiseri*, *E.* sect. *Olygotrichium*, and *E.* sect. *Karvinskia* (represented by *E. karvinskianus* DC.), in turn, form a well-supported clade distinct from all other *Erigeron* taxa included in the analysis. There is no evidence that *E. geiseri* has taxonomic affinity with members of *E.* sect *Quercifolium* or *E.* sect. *Geniculactis*. Those sections are so distant so as to preclude representation in Figure 5.

Alignment for the ITS plus ETS concatenated analysis for 24 *Erigeron* sequences resulted in a matrix 1254 bp in length. The phylogenetic analyses employed the GTR plus G model of molecular evolution and yielded trees similar in topology to the ITS-only analysis. The tree (Fig. 6) shows strong support for a monophyletic *E. geiseri* (1.0 Bayesian probability, 63% maximum likelihood bootstrap support), but also shows support for internal structure not present in the ITS-only analysis. Specifically, the 'S3' sample of coastal *E. geiseri* is shown as sister to the remaining four samples. The combined sequence matrix shows that the 'S3' sequence differs from 'S4' at 6 base positions, resulting in a genetic distance of 0.006. Sequences for 'S4', 'A1', 'A2', and 'A4' are virtually identical (mean genetic distance 0.0001).

The remainder of the topology (Fig. 6) is consistent with the ITS-only topology (Fig. 5). Internal structure of *E.* sect. *Phalacroloma* is supported with a basal *E. strigosus* var. *calcicola*, next divergent *E. strigosus* var. *dolomiticola*, then three haplotype clades within *E. strigosus* var. *strigosus* as previously described (Noyes, 2006). Support for *E.* sect. *Phalacroloma* plus *E. geiseri* increases with the addition of ETS sequence to 1.0 Bayesian

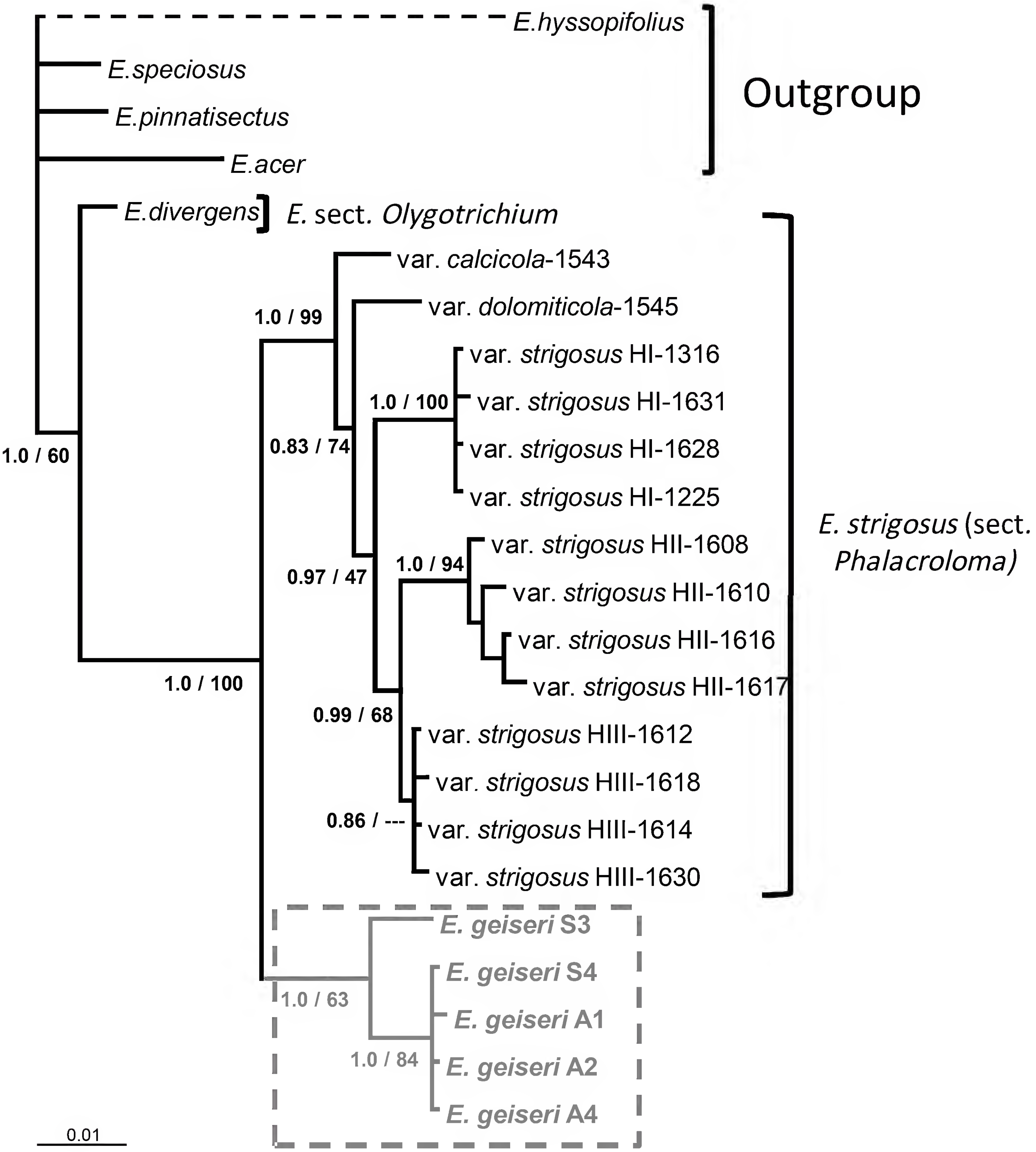
E.hyssopifolius
E.speciosus
E.pinnatisectus
E.acer
Outgroup
E.divergens
E. sect. Olygotrichium
var. calcicola-1543
var. dolomiticola-1545
var. strigosus HI-1316
var. strigosus HI-1631
var. strigosus HI-1628
var. strigosus HI-1225
var. strigosus HII-1608
var. strigosus HII-1610
var. strigosus HII-1616
var. strigosus HII-1617
var. strigosus HIII-1612
var. strigosus HIII-1618
var. strigosus HIII-1614
var. strigosus HIII-1630
E. strigosus (sect. Phalacroloma)
E. geiseri S3
E. geiseri S4
E. geiseri A1
E. geiseri A2
E. geiseri A4
1.0 / 99
1.0 / 100
0.83 / 74
1.0 / 60
0.97 / 47
1.0 / 94
1.0 / 100
0.99 / 68
0.86 / ---
1.0 / 63
1.0 / 84
0.01

Fig. 6. ITS plus ETS phylogeny for *Erigeron* sect. *Phalacroloma* and *Erigeron geiseri*. Phylogeny for 24 sequences (Appendix 2) generated using a GTR+G evolutionary model. Values at nodes are Bayesian probabilities and bootstrap percentages respectively. Sample designations for *E. geiseri* according to Table 1. Sample designations for *E. strigosus* follow Noyes (2006).

probability and 100% maximum likelihood bootstrap support. In addition, support for the alliance between *E.* sect. *Phalacroloma* (plus *E. geiseri*) and *E.* sect. *Olygotrichium* is retained.

DISCUSSION

Erigeron geiseri likely includes sexual diploid and polyploid apomictic populations

The pollen analysis and distribution map support the hypothesis that *E. geiseri* includes both sexual diploid and apomictic polyploid populations. The genetic similarity between samples is consistent with an evolutionary model in which apomixis and polyploidy originated from within *E. geiseri* (via auto- or segmental polyploid origin) and not via hybridization involving other taxa. Alternatively, apomixis has introgressed into *E. geiseri* from a related species, leaving no rDNA evidence of past ancestry. Sequence analysis of apomixis genes in *Erigeron* would be key for distinguishing these alternative hypotheses. However, this goal, for *Erigeron* or any other natural apomict, remains elusive (Hand & Koltunow 2014).

The distribution of putative diploid sexuals versus polyploid apomicts in *E. geiseri* shows a pattern typical for geographic parthenogenesis (Bierzychudek 1985) with sexual diploid populations with limited distribution occurring to the south, and with apomicts with much wider distribution extending northward. *Erigeron geiseri* is thus apparently similar to *E. strigosus* and *E. tenuis* (both *E.* sect. *Phalacroloma*) that feature narrowly distributed sexual diploid populations in the southeastern US, and widespread triploid and tetraploid apomicts extending northward (Noyes 2006; Groff 2010; Noyes & Givens 2013). Apomixis has also been documented for *E. annuus* (*E.* sect. *Phalacroloma*; Noyes & Givens 2013), as well as *E. divergens* (*E.* sect. *Olygotrichium*) of the western US, and also in *E. karvinskianus* (*E.* sect. *Karvinskia*) and so the trait is evidently common among species in these related sections.

Sexual diploid plants in *E.* sect. *Phalacroloma* thus far investigated have a relatively rare form of reproductive development, tetraspory, whereby meiosis of the megasporocyte yields a coenospore with four nuclei that each undergo mitotic divisions to yield a genetically mosaic female gametophyte (Noyes & Allison 2005). Tetraspory is thought to represent a temporal developmental shift in the timing of key meiotic events and may represent a predisposition toward the evolution of apomictic development (Carman 1997). Tetraspory is possibly common in *Erigeron*, perhaps more frequent than the classic monosporic 'Polygonum' type development that is characteristic of most Asteraceae (Noyes 2007). We would therefore predict that sexual diploid populations of *E. geiseri* would exhibit tetrasporic development and that apomicts would likely exhibit diplospory as is found in apomictic relatives. Chromosome number and reproductive developmental studies are warranted; the distribution map provided by this study will be a useful guide for locating populations. Further field study also may be warranted to investigate genetic and morphological differentiation between coastal and interior sexual diploid populations.

Erigeron geiseri is closely allied with *E.* sect. *Phalacroloma*

Our analysis of nrDNA sequence shows that samples of *Erigeron geiseri* form a monophyletic group that is sister to *E. strigosus* and allies that constitute *E.* sect. *Phalacroloma*. Shinners (1947) hypothesized that *E. geiseri* was related to *E. coronarius* based on the similarities including a biseriate few-bristled pappus, conical receptacle, and annual habit. The later species presently serves as the type of *Erigeron* sect. *Geniculactis*, a group of six species restricted to Mexico and adjacent southern Arizona (Nesom 2008). Our ITS analysis included a sample for *E. coronarius*, however, and no affinity between the two species was supported (Fig. 5). The classification of *E. geiseri* in *E. sect. Quercifolium* (Nesom 2008) is also not supported. Our ITS sample included *E. quercifolius* (the type species of the section), *E. philadelphicus*, *E. dryophyllus*, and *E. veracruzensis* of the section. While these four species form a monophyletic clade, they are not closely related to *E. geiseri* (Fig. 5; Noyes 2000). Instead, an affinity of *E. geiseri* with *E.* sect. *Phalacroloma* is supported (Fig. 6), a finding foreshadowed by earlier discussion noting morphological similarities between *E. geiseri* and *E. tenuis* (Nesom 1987; Nesom 2008). Based on nrDNA sequence, sexual diploid *E. tenuis* resides as a clade within *E. strigosus* with some individuals exhibiting both 'tenuis-like' and 'strigosus-like' nrDNA haplotypes consistent with recent hybridization between the two taxa (Noyes 2000; Groff 2010). *Erigeron geiseri* and *E. tenuis*, along with *E. turnerorum* (of Nuevo Leon, Mexico) and *E. tenellus* (of extreme southern Texas and adjacent Mexico) share a suite of floral and vegetative characters, which together with geographic parapatry, is consistent with close evolutionary relationship (Nesom 1987). *Erigeron geiseri* is distinct from *E. tenuis*, and more similar to *E. turnerorum* and *E. tenellus*, because of its tap-rooted, annual habit. *Erigeron tenuis* and other *E.* sect. *Phalacroloma* (*E. strigosus* and *E. annuus*) are fibrous-rooted and longer lived. *Erigeron geiseri*, *E. tenellus*, and *E. turnerorum* are distinct from the other sixteen species classified as *E.* sect. *Quercifolium* (Nesom 2008) in being the only tap-rooted taxa. We recommend based on our results that *E. geiseri* be reclassified as a member of *E.* sect. *Phalacroloma*. By extension, based on morphological considerations, we would predict that DNA study will show that *E. tenellus* and *E. turnerorum* are also members of *E.* sect. *Phalacroloma*.

While our conclusion regarding the taxonomic reclassification of *E. geiseri* is well supported by the ITS and ETS sequence, we must add the caveat that our phylogeny is nonetheless based on data from a single gene region. Although ITS has been a mainstay in lower level plant systematics for nearly two decades (Feliner & Rosello 2007) and has been proposed to be included, along with select chloroplast gene regions, as a component of a universal plant barcode (China Plant BOL Group 2011), it nonetheless potentially reflects a biased portrait of relationship. It has long been appreciated that because of phenomena such as recombination, hybridization, lineage sorting, and horizontal gene transfer, different genes may yield topologically incongruent phylogenies (Wendel & Doyle 1998). The problem is exemplified by recent work in *Symphyotrichum* (also tribe Astereae) in which study of ITS plus ETS on the one hand, and the unlinked 5S nrDNA nontranscribed spacer on the other, revealed seven phylogenetic disagreements attributed to three reticulate evolutionary events involving six different species (Morgan & Holland 2012). Multigene, genome wide phylogenetic reconstruction, successfully implemented for study of the highest levels of plant diversity (e.g., Angiosperm Phylogeny Group 2009; Finet et al. 2010), remains elusive at lower taxonomic levels for many groups owing to the difficulty of identifying strictly orthologous single copy nuclear genes (Feliner & Rosello 2007). Nonetheless, we anticipate advances from the study of a small number of nuclear markers plus the further refinement of enrichment techniques coupled with Next Generation Sequencing methodologies (Mandel et al. 2014) to soon provide a means for generating robust phylogenies for species rich complex groups as represented by North American *Erigeron*.

APPENDIX 1

Taxa and GenBank numbers for 76 ITS sequences of Astereae sect. Conyzinae used for phylogenetic analysis (AF046986:AF046992; AF118478:AF118487; AF118491:AF118545; AY871316; AY871318; AY871323; AY871333). GenBank accession numbers for five ITS sequences for Erigeron geiseri given in Table 1.

Aphanostephus ramossissimus [AF046990]; Aph. skirrhobasis [AF118521]; **Apopyros** warmingii [AF118511]; **Conyza** apurensis [AF118482]; C. bonariensis [AF118513]; C. canadensis [AF046987]; C. chilensis [AF118510]; C. floribunda [AF118514]; C. ramosissima [AF118484]; **Erigeron** acris [AF118496]; E. aliceae [AF118541]; E. aphanactis [AF118531]; E. arenarioides [AF118528]; E. argentatus [AF118506]; E. barbellatus [AF118536]; E. bellioides [AF118522]; E. borealis [AF118495]; E. caespitosus [AF118481]; E. cinereus [AF118502]; E. compositus [AF118537]; E. coronarius [AF118520]; E. divergens [AF118485]; E. dryophyllus [AF118524]; E. eatonii [AF118540]; E. eruptens [AF118543]; E. fernandezianus [AF118515]; E. flettii [AF118503]; E. foliosus [AF118532]; E. formosissimus [AF118478]; E. fraternus [AF118518]; E. galeotii [AF118519]; E. glabellus [AF118498]; E. glaucus [AF118499]; E. grandiflorus [AF118494]; E. humilus [AF118504]; E. hyssopifolius [AY871316]; E. inornatus [AF118533]; E. kachinensis [AF118480]; E. karvinskianus [AF118487]; E. leiomerus [AF118492]; E. lepidopodus [AF118545]; E. leptorhizon [AF118483]; E. linearis [AF118534]; E. lonchophyllus [AF118505]; E. maximus [AF118509]; E. neomexicanus [AF118544]; E. ochroleucus [AF118539]; E. philadelphicus [AF046989]; E. pinnatisectus [AF118501]; E. pinnatus [AF118517]; E. podophyllus [AF118542]; E. pulchellus [AF118500]; E. pumilus [AF118530]; E. pygmaeus [AF118526]; E. quercifolius [AF118525]; E. religiosus [AF118486]; E. rhizomatus [AF046992]; E. rosulatus-1 [AF118512]; E. rosulatus-2 [AF118516]; E. scoparioides [AF118527]; E. scopulinus [AF118497]; E. simplex [AF118493]; E. speciosus [AF118479]; E. strigosus var. calcicola [AY871318]; E. strigosus var. dolomiticola [AY871323]; E. strigosus var. strigosus [AY871333]; E. tener [AF118535]; E. tweedyi [AF118529]; E. uniflorus [AF046988]; E. ursinus [AF118491]; E. utahensis [AF118507]; E. vagus [AF118538]; E. veracruzensis [AF118523]; E. wislizenii [AF046991]; **Hysterionica** jasionoides [AF046986]; **Neja** filiformis [AF118508].

APPENDIX 2

Taxa and GenBank numbers for 19 ITS plus ETS sequences used for phylogenetic analysis of Erigeron sect. Phalacroloma and E. geiseri (**ITS:** AF118479, AF118496, AF118501, AY871316:AY871318, AY871323:AY871330, AY871333, AY871334, AY871340, AY871341, AY871553; **ETS:** AY871355:AY871360, AY871365:AY871372, AY871375, AY871376, AY871382, AY871383, AY871744). GenBank accession numbers for five ITS plus ETS sequences for E. geiseri given in Table 1.

Outgroups:
Erigeron acris [AF118496 (ITS), AY871356 (ETS)]; ***E. hyssopifolius*** [AY871316, AY871355]; ***E. pinnatisectus*** [AF118501, AY871357]; ***E. speciosus*** [AF118479, AY871358]
Erigeron sect. Olygotrichium:
Erigeron divergens [AY871317, AY871359]
Erigeron sect. Phalacroloma:
Erigeron strigosus* var. *calcicola [AY871318, AY871360]; ***E. strigosus* var. *dolomiticola*** [AY871323, AY871365]; ***E. strigosus* var. *strigosus* rDNA haplotype I**: [AY871325, AY871367], [AY871326, AY871368], [AY871327, AY871369], [AY871324, AY871366]; **rDNA haplotype II**: [AY871328, AY871370], [AY871553, AY871744], [AY871329, AY871371], [AY871330, AY871372]; **rDNA haplotype III** [AY871333, AY871375], [AY871334, AY871376], [AY871340, AY871382], [AY871341, AY871383].

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NEW COMBINATIONS IN *CORYPHANTHA* AND *ESCOBARIA* (CACTACEAE)

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ABSTRACT

Most cactus taxonomists accept *Coryphantha organensis* as a synonym of *Coryphantha orcuttii*. Therefore, at infraspecific rank, *Coryphantha orcuttii* needs to be considered a variety (not a subspecies) of *C. sneedii* because *C. orcuttii* is partially sympatric with the type subspecies/variety of *C. sneedii* at Anthony's Nose, Doña Ana County, New Mexico. This requires a new combination for *Coryphantha orcuttii* and *EscobarIa orcuttii* at the rank of variety, depending on whether you consider *Escobaria* to be a separate genus versus subgenus/section of *Coryphantha*. The two new combinations are: **Coryphantha sneedii** var. **orcuttii** comb. et stat. nov. and **Escobaria sneedii** var. **orcuttii** comb. et stat. nov.

RESUMEN

La mayoría de los taxónomos de cactus aceptan *Coryphantha organensis* como sinónimo de *Coryphantha orcuttii*. Sin embargo, a nivel infraespecífico, *Coryphantha orcuttii* necesita ser considerado una variedad (no una subespecie) de *C. sneedii* porque *C. orcuttii* es parcialmente simpátrico con la subespecie/variedad tipo de *C. sneedii* en Anthony's Nose, Doña Ana County, Nuevo México. Esto requiere una nueva combinación para *Coryphantha orcuttii* y *EscobarIa orcuttii* en el rango de variedad, dependiendo si se considera o no que *Escobaria* sea un género separado del subgénero/sección *Coryphantha*. Las dos nuevas combinaciones son: **Coryphantha sneedii** var. **orcuttii** comb. et stat. nov. y **Escobaria sneedii** var. **orcuttii** comb. et stat. nov.

INTRODUCTION

While drafting a manuscript on cacti that survive unprotected outdoors in Canada (Gorelick et al. 2015), I wanted to use a combination for a plant taxon in the *Coryphantha sneedii* complex that has not been published. A few of the varieties/subspecies of *C. sneedii* (Britton & Rose) A. Berger, including *C. orcuttii* (Rose ex Orcutt) Zimmerman and the type variety/subspecies of *C. sneedii* Britton & Rose, are the only cacti that I have successfully grown unprotected in both Tempe, Arizona, USA where summer temperatures occasionally hit +50°C, and Ottawa, Ontario, Canada where winter temperatures often hit -30°C, and that is without wind chill.

The type subspecies/variety of *Coryphantha sneedii* appears to be ancestral (Baker 2004) to all other subspecies, varieties, and forms, which are spread out radially in all directions (Zimmerman 1985): '*leei*' and '*guadalupensis*' to the east; '*villardii*' to the northeast; '*sandbergii*' to the north; '*orcuttii*' to the west; two of Allan Zimmerman's unnamed varieties to the south; and '*albicolumnaria*' to the southeast. But, when first described, it was not obvious whether these infraspecific taxa in the *C. sneedii* complex were partially sympatric or allopatric with one another hence it was not obvious whether these were subspecies or varieties (or merely just forms).

Subspecies versus variety

Usage of 'subspecies' and 'variety' has at times been confused and has had a changing history in the more than two centuries since both terms have been in existence (Clausen 1941; Stuessy 2009). Meanings of these two infraspecific categories gradually stabilized by the mid 1900s (Clausen 1941), but there still is some contention about their usage even to this day (Stuessy 2009). I therefore begin by describing Clausen's (1941) definitions given in a paper titled *On the use of the terms 'subspecies' and 'variety'*, followed by Hamilton and Reichard's (1992) paper titled *Current practice in the use of subspecies, variety, and forma in the classification of wild plants*,

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followed by Turner and Nesom's (2000) paper whose title begins *Use of variety and subspecies*, and finally Stuessy's (2009) definitions of subspecies and variety from his widely used text titled *Plant taxonomy*.

Subspecies are comprised of individuals with a consistent suite of morphological traits that differ from other individuals of the species due to geographic, ecological, or physiological isolation (Clausen 1941). Geographic and ecological isolation are easier for taxonomists to discern than physiological isolation, so I ignore physiology herein. Both varieties and subspecies have consistent morphological features. If that morphology is due to geographic or ecological variation, then Clausen (1941) called that taxon a subspecies, otherwise he called it a variety.

Hamilton and Reichard (1992: 491) "recogniz[ed] subspecies for groups primarily with greater geographic/ecologic distinctness than varieties..." Thus, like Clausen (1941), they required some modicum of geographic or ecological isolation. Hamilton and Reichard (1992) also noted that European plant taxonomists tend to use 'subspecies' more often, while North American plant taxonomist tend to use 'variety' more often.

Turner and Nesom (2000: 258) stated that, "use of the subspecies rank may point to larger patterns of variation and/or coherence within the species. This use of infraspecific categories finds support in the ICBN, which implies that the term subspecies is used for clustering varieties."

Stuessy (2009) did not so much define subspecies and variety, but provided a list of characters that are useful in distinguishing the two. These characters are in the following categories: morphology, geographic overlap, genetic divergence, likelihood of naturally hybridizing, and fertility of hybrids. For the *Coryphantha sneedii* complex, we really only know about geographic overlap and morphology, so can ignore the other characteristics, meaning that difference between subspecies and variety still depend on both morphology and geographical isolation, as was true three-quarters of a century ago (Clausen 1941). For Stuessy (2009), subspecies have a larger number of traits with morphological differences than do varieties. For Stuessy (2009), subspecies are largely allopatric or peripatric, while varieties can have somewhat overlapping distributions.

Some authors (e.g., Corogin & Judd 2014, in this journal) even seem to require that subspecies be allopatric. By contrast, "In American taxonomy, possibly the most widely accepted concept regarding varieties is that … varieties are expected to overlap in distribution …" (A. Michael Powell, pers. comm., 27 Dec 2014). Several authors outside of North America also require varieties, but not subspecies, to have overlapping distributions, e.g., "It is generally held that the rank of subspecies should be used for populations of a species that have several morphological differences and are geographically and/or ecologically separated, whereas varieties, also with some morphological differences, overlap in their distribution" (Newton & Thiede 2015: 30). Therefore in attempting to decide whether members of the *Coryphantha sneedii* complex are subspecies or varieties, we need to focus on number of morphological differences and especially on geographic isolation.

Coryphantha versus *Escobaria*

Should *Coryphantha sneedii* be placed into the segregate genus *Escobaria* Britton & Rose? From a purely formal view, this does not matter here because *Coryphantha sneedii* and *Escobaria sneedii* (Britton & Rose) A. Berger have both been validly published. I leave both options open, even though I consider *Escobaria* to be a subgenus [*Coryphantha* (Engelm.) Lem. subgenus *Escobaria* (Britton & Rose) A. Berger]. Other authors consider *Escobaria* to be a section of *Coryphantha* [*Coryphantha* section *Escobaria* (Britton & Rose) H.E. Moore] This portion of the paper should thus be considered dicta, i.e., this debate does not affect the conclusions of the rest of this paper because I will make combinations in both genera. Debates over whether *Escobaria* is a genus or a subgenus or a section of *Coryphantha* will probably continue for many years.

Any attempt to segregate *Escobaria* from *Coryphantha* will probably result in paraphyly. Thus the *Flora of North American* (Parfitt & Gibson 2003; Zimmerman & Parfitt 2003) subsumes *Escobaria* under the earlier valid genus epithet *Coryphantha*, as did Benson (1982), Powell and Weedin (2004), and most other North American authors. Paraphyly provides a reason to dismiss *Escobaria*, even though there are morphological differences, albeit not consistent morphological differences, between taxa considered to be *Escobaria* versus *Coryphantha*. Subgenus *Escobaria* has pitted seeds, whereas subgenus *Coryphantha* does not (Anderson 2001; Zimmerman & Parfitt 2003; Dicht & Lüthy 2005; Hunt et al. 2006), except for *C. gracilis* L. Bremer & A.B. Lau

(Taylor 1986; Dicht & Lüthy 2005). Most taxa in subgenus *Coryphantha* contain extra-floral nectary glands, whereas all taxa in subgenus *Escobaria* lack these glands (Zimmerman & Parfitt 2003; Dicht & Lüthy 2005). Subgenus *Escobaria* generally has smaller flowers, fruits, and seeds than subgenus *Coryphantha* (Castetter et al. 1975). For these reasons, most European authors consider *Escobaria* to be a valid genus (Dicht & Lüthy 2005), even if many North Americans do not (Zimmerman & Parfitt 2003).

But, with the logic of trying to avoid paraphyly, there may also be reason to dismiss *Coryphantha* as a genus and subsume it under *Mammillaria*. A phylogenetic analysis based solely on chloroplast markers showed *Coryphantha, Escobaria, Pelecyphora* Ehrenb., *Ortegocactus* Alexander, and *Neolloydia conoidea* Britton & Rose to all be embedded within *Mammillaria* Haw. (Butterworth & Wallace 2004), i.e., making both *Escobaria* and *Coryphantha* paraphyletic. However, it is not obvious how much weight to place on that 2004 molecular study because chloroplast inheritance is not always maternal in the Cactaceae (Corriveau & Coleman 1988; Gorelick 2014) and there is probably some alloploidy in this clade, e.g., the tetraploid *Coryphantha missouriensis* (Scheer) Britton & Rose (Weedin & Powell 1980), indicating the need for reticulate phylogenies. I therefore lean towards retaining use of *Coryphantha* as a genus, subsuming all *Escobaria* therein, but could be persuaded otherwise after more systematic analyses are performed based on both genotype and phenotype, especially if nuclear markers are used in constructing molecular phylogenies.

Coryphantha orcuttii, C. organensis, C. sneedii

In New Mexico, *Coryphantha orcuttii* ranges from the Peloncillo Mountains to the Florida Mountains (Ferguson 1998a). This taxon is also found in neighboring Arizona, Chihuahua, and Sonora. This range extends to the Organ Mountains if *C. organensis* Zimmerman is considered a synonym of *C. orcuttii* (see below). *C. orcuttii* and *C. sneedii* var. *albicolumnaria* (Hester) A.D. Zimmerman are by far the most widespread taxa in the *Coryphantha sneedii* complex.

The type subspecies/variety of *Coryphantha sneedii* is endemic to the Franklin Mountains in El Paso County, Texas, the southern end of the Organ Mountains in Doña Ana County, New Mexico, and some of the mountains between the two, e.g., Bishop's Cap and Anthony's Nose.

Given the huge amount of morphological variation and geographic range in the *Coryphantha sneedii* complex (Zimmerman 1985), it makes sense to follow the modern consensus amongst cactus taxonomists that *C. orcuttii* should be considered an infraspecific form of *C. sneedii* (Zimmerman & Parfitt 2003; Baker 2004; Powell & Weedin 2004; Hunt et al. 2006). Thus, *Coryphantha orcuttii* is usually considered to be a synonym of *Escobaria sneedii* Britton & Rose subsp. *orcuttii* (Boed.) Lüthy, but here I argue that a subspecies designation is inappropriate for this taxon. *Coryphantha orcuttii* seems to be morphologically indistinguishable from *Coryphantha organensis* (synonym: *Escobaria organensis* (Zimmerman) Castetter, P. Pierce, & K.H. Schwer.) (Ferguson 1998 a,b). The only morphological trait that supposedly consistently distinguishes *Coryphantha organensis* from the rest of the *C. sneedii* complex is a slight yellowish cast to spine color in *C. organensis* (Zimmerman 1972a; Taylor 1986; Ferguson 1998b). Color is typically a variable trait, often encoded by an allelic shift at a single genetic locus, thus at most warranting designation as a form, not a variety, let alone a subspecies (Stuessy 2009). Therefore many authors consider *C. organensis* to be a synonym of *C. orcuttii*, itself possibly subsumed under *C. sneedii* (e.g., Lüthy 1999; Hunt et al. 2006; U.S. Geological Survey's 'Integrated Taxonomic Information System' (ITIS; http://www.itis.gov/)). If *C. organensis* is a synonym of *C. orcuttii*, then the subspecies designation of *C. orcuttii* as *Escobaria sneedii* subsp. *orcuttii* and the hitherto unpublished combination *Coryphantha sneedii* subsp. *orcuttii* cannot be valid because *C. organensis* and *C. sneedii* subsp. *sneedii* have overlapping distributions at Anthony's Nose (Ferguson 1998 b,c; Gorelick 2006), which straddles the Texas-New Mexico border, and probably also have overlapping distributions at North Anthony's Nose ('nose' is an idiosyncratic local term for these mountains). Anthony's Nose and North Anthony's Nose are separated by Anthony Gap, through which runs New Mexico State Highway 404, at the northern end of the Franklin Mountains (Doña Ana County, New Mexico and El Paso County, Texas), south of Fillmore Pass and the Organ Mountains. Clausen (1941), Hamilton and Reichard (1992), Stuessy (2009), and Corogin and Judd (2014) all require allopatry or peripatry between two or more subspecies of a given species. Turner and Nesom (2000) do not require allopatry or peripatry between subspecies, but insist that a subspecies be an aggregate of two or more varieties. However, that is not the case here because *C. organensis* is a synonym of *C. orcuttii* and there are no other obvious varieties in the *Coryphantha sneedii* complex west of the franklin and organ Mountains. The only possible exceptions are *Escobaria orcuttii* var. *macraxina* Castetter, P. Pierce & K.H. Schwer. from the Big Hatchet Mountains and *Escobaria orcuttii* var. *koenigii* Castetter, P. Pierce & K.H. Schwer. from the Florida Mountains (Castetter et al. 1975; Taylor 1986), but nobody nowadays, including me, accepts these as valid varieties or even consistent forms or morphs. Therefore a subspecies designation is inappropriate for *Coryphantha orcuttii* seemingly regardless of usage of the designation 'subspecies'.

Instead of a subspecies designation, should *Coryphantha orcuttii* be considered a variety of *C. sneedii*? *Coryphantha orcuttii* is consistently morphologically different from *C. sneedii* subsp. *sneedii*, despite these two taxa being partially sympatric at Anthony's Nose. *Coryphantha sneedii* has many more shoots, sometimes hundreds more, than *C. orcuttii*, which is often solitary (Ferguson 1998a,c; Anderson 2001; Hunt et al. 2006). *Coryphantha sneedii* has smaller shoots (2.5–10 × 1.0–2.5 cm) than *C. orcuttii* (15 × 6–9 cm) (ibid). *Coryphantha sneedii* has shorter central spines (4.5–10 mm) than *C. orcuttii* (9–22 mm) (ibid). Seemingly the only viable alternative is therefore to consider *Coryphantha organensis* to be a synonym of *C. orcuttii* and then to classify *C. orcuttii* as a variety of either *Coryphantha sneedii* or *Escobaria sneedii* (not a variety of *Coryphantha strobiliformis* (Poselg.) Moran, where the name *orcuttii* currently exists at the rank of variety). This requires one of the following two new combinations, the choice of which depends on whether or not you consider *Escobaria* to be a separate genus of subgenus/section of *Coryphantha*:

Coryphantha sneedii var. **orcuttii** (Boed.) Gorelick, comb. et stat. nov. Basionym: *Escobaria orcuttii* Bödecker, Ein Mammillarien Vergleichs-Schlüssel 17. 1933. Type: U.S.A. New Mexico. Hidalgo Co.: Peloncillo Mountains, near Granite Pass, Mar 1926, *J.N. Rose s.n.* (lectotype, designated by Benson 1969: 26: DS).

Coryphantha strobiliformis (Poselg.) Moran var. *orcuttii* (Rose ex Orcutt) L.D. Benson, Cacti Ariz. ed. 3, 26. 1969.
Coryphantha orcuttii (Rose ex Orcutt) Zimmerman, Cact. Succ. J. (US) 44:156. 1972.
Coryphantha organensis Zimmerman, Cact. Succ. J. (US) 44:114. 1972.
Escobaria organensis (Zimmerman) Castetter, P. Pierce & K.H. Schwer., Cact. Succ. J. (US) 47:60. 1975.
Escobaria sneedii Britton & Rose subsp. *orcuttii* (Boed.) Lüthy, Kakt. and. Sukk. 50:278. 1999.
Escobaria sneedii Britton & Rose subsp. *organensis* (Zimmerman) Lüthy, Kakt. and. Sukk. 50:278. 1999.

Escobaria sneedii var. **orcuttii** (Boed.) Gorelick, comb. et stat. nov. Basionym: *Escobaria orcuttii* Bödecker, Ein Mammillarien Vergleichs-Schlüssel 17. 1933. Type: U.S.A. New Mexico. Hidalgo Co.: Peloncillo Mountains, near Granite Pass, Mar 1926, *J.N. Rose s.n.* (lectotype, designated by Benson 1969: 26: DS).

Coryphantha strobiliformis (Poselg.) Moran var. *orcuttii* (Rose ex Orcutt) L.D. Benson, Cacti Ariz. ed. 3, 26. 1969.
Coryphantha orcuttii (Rose ex Orcutt) Zimmerman, Cact. Succ. J. (US) 44:156. 1972.
Coryphantha organensis Zimmerman, Cact. Succ. J. (US) 44:114. 1972.
Escobaria organensis (Zimmerman) Castetter, P. Pierce & K.H. Schwer., Cact. Succ. J. (US) 47:60. 1975.
Escobaria sneedii Britton & Rose subsp. *orcuttii* (Boed.) Lüthy, Kakt. and. Sukk. 50:278. 1999.
Escobaria sneedii Britton & Rose subsp. *organensis* (Zimmerman) Lüthy, Kakt. and. Sukk. 50:278. 1999.

According to Zimmerman (1972b), Joseph N. Rose in 1926 named this taxon '*Neolloydia orcuttii*' (*nomen nudum*) for a specimen collected by Charles Russell Orcutt from Granite Pass, near the New Mexico-Arizona border, in the Peloncillo Mountains, and Rose did not designate a type. Granite Pass in the Peloncillo Mountains of New Mexico is almost certainly now known as "Granite Gap." I have been unable to trace when this wording change occurred other that it was on or before the mid 1950s (Gillerman 1957). The global unique identifier for the lectotype is "CAS:DS:307410." The California Academy of Sciences website (http://collections.calacademy.org/bot/) gives a collection date of 28 March 1926 for this specimen. According to Roy Mottram (pers. comm., 14 Feb 2014), Rose also provisionally published the combination '*Escobaria orcutti*' for this plant taxon in Cactography 4(1):5, 1926. Spelling of *orcutti* with a single '*i*' also appears in the documentation for *Coryphantha strobiliformis* in Benson (1982: 963), probably as a typographical error.

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SCLERIA BELLII (CYPERACEAE), A DISTINCTIVE AND UNCOMMON NUTSEDGE FROM THE SOUTHERN U.S., CUBA, AND MEXICO

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ABSTRACT

A new species of *Scleria* (Cyperaceae) is described from the southeastern United States, Cuba, and Mexico. Although widespread, known populations are few and scattered, with 14 in the United States from North Carolina to Texas, and one each in Cuba and Mexico. In the United States, 12 populations are found on the outer Coastal Plain, and two in the Carolina Piedmont. At known sites, soils are wet, and several populations occur in rare and unusual habitats with acidic pH and a calcareous influence.

RESUMEN

Se describe una nueva especie de *Scleria* (Cyperaceae) del sureste de Estados Unidos, Cuba, y México. Aunque muy extendida, las poblaciones conocidas son pocas y esparcidas, con 14 en los Estados Unidos desde Carolina del Norte a Texas, y una en Cuba y otra en México. En los Estados Unidos, 12 poblaciones se encuentran en la llanura costera externa, y dos en el piedemonte de Carolina. En los sitios conocidos, los suelos son húmedos, y varias poblaciones se dan en hábitats raros e inusuales con pH ácido y una influencia calcárea.

INTRODUCTION

A distinctive nutsedge sharing characteristics of the *Scleria ciliata* complex was found in southeastern North Carolina during natural area inventories for the state's Natural Heritage Program in the 1990s. Since that discovery, the new taxon was treated as "*Scleria* species 1" in Weakley (2013). Subsequently, more than 1,200 herbarium collections of taxa in the *S. ciliata* complex were examined from AUA, BRIT (including SMU and VDB), DUKE, FLAS, FSU, GH, LSU, MO, NCSC, NCU, NY, US, and USCH. As a result, 16 populations of the new nutsedge are now known from Florida, Georgia, Louisiana, North Carolina, South Carolina, Texas, Cuba, and Mexico (Fig. 1). Among the 14 populations known from the U.S., 12 are located on the outer Atlantic and Gulf Coastal Plain, and two are from the Carolina Piedmont. This widespread but apparently rare nutsedge is here described as a new species.

Scleria bellii LeBlond, sp. nov. (**Fig. 2**). Type: UNITED STATES. North Carolina. Onslow Co.: in moderately dense graminoid-forb ground cover of wet savanna, formerly known as Haws Run Mitigation Site, now part of Maple Hill Savannas State Natural Area, near Onslow/Pender county line between Sandy Run Swamp and Shelter Swamp Creek, 6 Jun 2013, *R.J. LeBlond 6958* (holotype: NCU; isotypes: AUA, BRIT, FLAS, FSU, GH, LSU, MO, NY, US, USCH).

Achene body smoothish with broad low rises, a few retrorse papillae at the very base; achene including hypogynium 2.5–3.2(–3.4) mm long, 2.3–2.7 mm wide; hypogynium basal rim 1.4–1.8(–2.1) mm wide; tubercles (4–)6.

Plants cespitose, few to several culms closely spaced along rhizomes 0.5–1 cm thick; culms (40–)60–100 cm long, 2–5.5 mm wide at base (including sheaths); surface of culm and sheaths glabrous between ciliate angles (culm sometimes puberulent between angles just below inflorescence); larger leaf blades 10–60 cm long, (2.5–)3–7 mm wide, ciliate along margins and primary nerves, glabrous between nerves (sometimes pubescent with stiff trichomes between nerves on abaxial surface), lacking fine puberulent hairs; inflorescence of terminal and axillary fascicles, the terminal fascicle of two closely-spaced clusters, the internode about 1 cm, the proximal cluster smaller; axillary fascicle one (-two), comprised of a single cluster; internode between terminal and axillary fascicles (6–)18–48(–56) cm; primary bract of terminal fascicle 2–5 mm wide, the longer cilia 1.1–2.2 mm; pistillate scales glabrous except for ciliate keel, the cilia 0.5–1 mm long; mature achenes in-

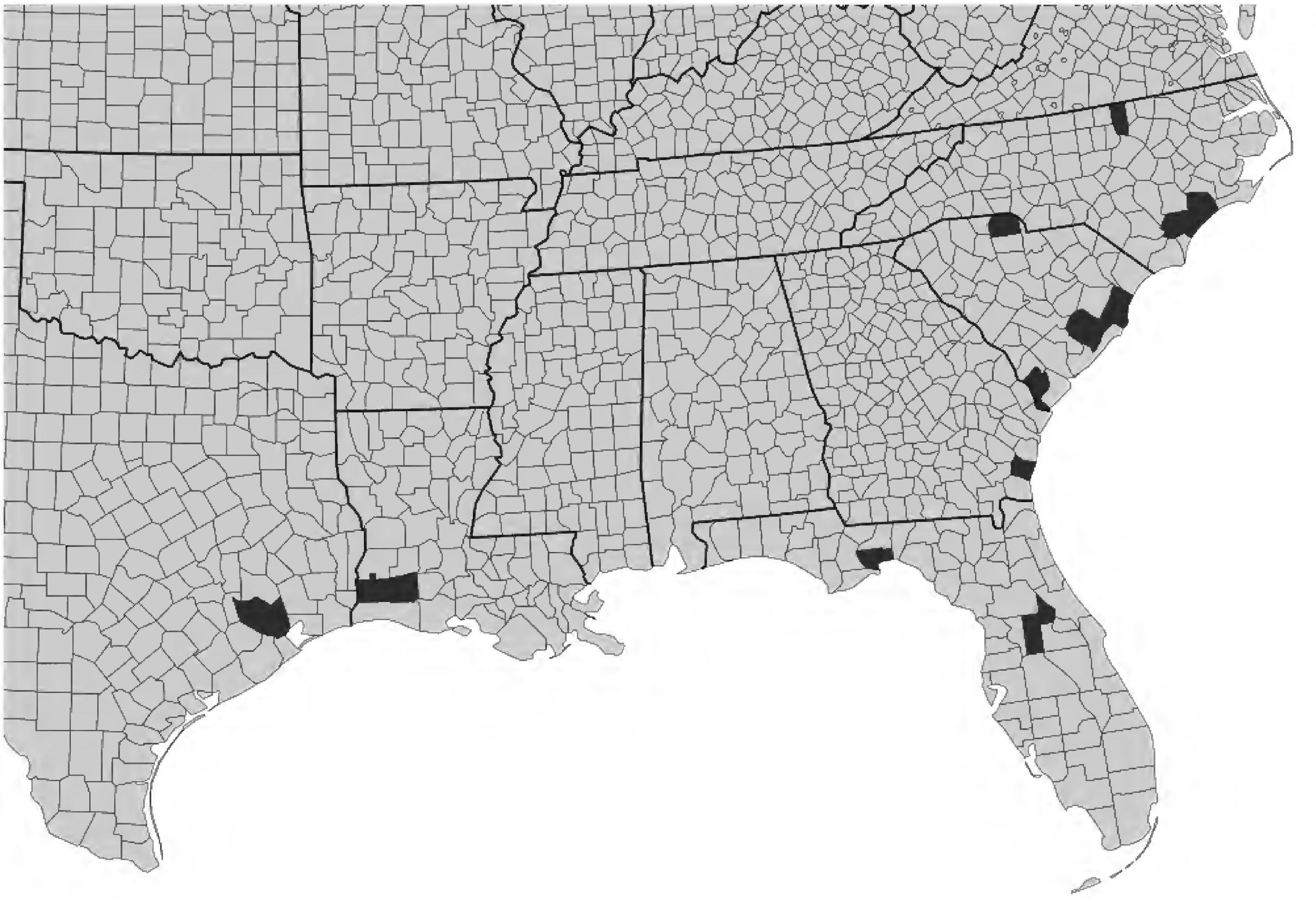
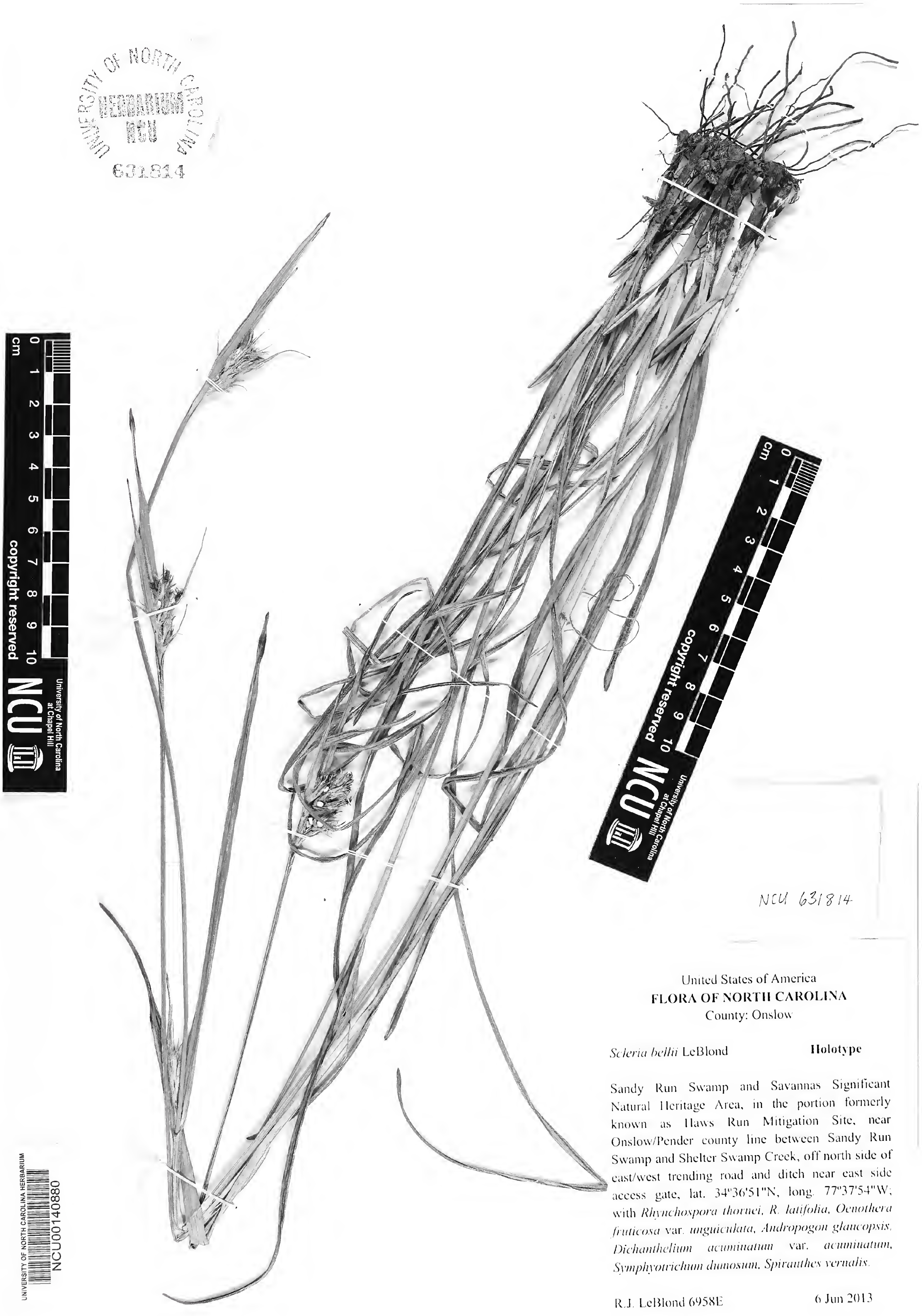


Fig. 1. *Scleria bellii* range map. Also known from one site each in Cuba and Mexico.

cluding hypogynium 2.5–3.2(–3.4) mm long by 2.3–2.7 mm wide; achene body bony white, smoothish with broad low rises, sometimes with faint transverse ridging, epapillate except for a few retrorse papillae at the very base (these minutely setulose distally); hypogynium basal rim tan to light brown, 1.4–1.8(–2.1) mm wide, 0.1–0.2(–0.3) mm long; tubercles (4–)6.

Etymology.—The specific epithet honors C. Ritchie Bell (1921–2013), scientist, teacher, co-author of the landmark *Manual of the Vascular Flora of the Carolinas* (Radford et al. 1968), and a founder and first director of the North Carolina Botanical Garden.

Additional specimens examined (PARATYPES unless otherwise indicated), representing all known populations: **CUBA. Santa Clara:** 4 Sep 1903, *Britton & Wilson 325* (NY!). **MEXICO. Jalisco:** abundante, 8 km al SE del Rancho El Mortero, municipio de Mezquitic, hab. bosque de Pinus leiophylla y Quercus spp., 5 Nov 1963, *Rzedowski 17703* (BRIT!). **UNITED STATES. FLORIDA. Lake Co.:** clay land, vicinity of Eustis, 1–15 Apr 1894, *Nash s.n.* (US!). **Wakulla Co.:** frequent in somewhat overgrown, but mowed area under powerlines along walking-bike trail just S of hiway 98 and ca. 0.2 mi W of rte 363 (Woodville hiway), ca. 1 air mile NW of town of St. Marks, 18 May 1991, *L.C. Anderson 13,398* (FSU!); frequent in moist, peaty sand with *Stillingia aquatica* (few low *Ilex* and *Myrica*) in clearing under powerlines along walking-bike trail just S of hiway 98 and W of rte 363 (Woodville hiway), ca. 1 air mile NNW of town of St. Marks, 3 Jun 1991, *L.C. Anderson 13,434* (FSU!, CLEMS). **GEORGIA. Glynn Co.:** replanted pine flatwoods 1.5 mi. w. of Altamaha River on co. rd. 620 to Everett City, 21 Jul 1966, *Bozeman 6313* (NCU!). **LOUISIANA. Calcasieu Par.:** coastal prairie remnant dominated by *Schizachyrium tenerum* and *S. scoparium, Rhynchospora* spp. conspicuous, *Rudbeckia texana* common, SW corner of Dennis Rd & Boudoin Rd., S of LA 108, E of LA 27, 2.2 mi S of jct. w/I-10, 14 May 2008, *Reid et al. 6539* (LSU!). **Jefferson Davis Par.:** low prairies, Jennings, 15 May 1915, *E.J. Palmer 7635* (MO!, US!). **NORTH CAROLINA. Granville Co.:** Camp Butner, a collection made during a floristic study of Iredell soil in central Piedmont of N.C., 25 Aug 1951, *Batson 543* (DUKE!, NY!). **Onslow Co.:** Sandy Run Swamp Powerline Savanna, Cooleys Meadowrue Powerline Survey Site, 4 Jun 1995, *LeBlond 4254* (NCU!); formerly Haws Run Mitigation Site, now part of Maple Hill Savannas State Natural Area, near Onslow/Pender county line between Sandy Run Swamp and Shelter Swamp Creek, 13 Jun 1996, *LeBlond 6951,* 17 June 1996, *LeBlond 4572*, 26 May 1998, *LeBlond 4980,* 20 Jul 1998, *LeBlond 5023,* 11 Jul 2000, *LeBlond 5363,* 14 Jun 2003, *LeBlond 5772* (TOPOTYPES: NCU!). **Pender Co.:** McLean Savanna, near southwestern edge of Holly Shelter Game Land, about 0.7 mile north-northeast of confluence of Catskin Creek and Trumpeter Swamp, 18 Aug 1997, *LeBlond & J. Taggart 4835* (NCU!); 20 Jun 2007, *LeBlond 6420 et al.* (NCU!). **SOUTH CAROLINA. Berkeley Co.:** Francis Marion Na-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United States of America
FLORA OF NORTH CAROLINA
County: Onslow

Scleria bellii LeBlond **Holotype**

Sandy Run Swamp and Savannas Significant Natural Heritage Area, in the portion formerly known as Haws Run Mitigation Site, near Onslow/Pender county line between Sandy Run Swamp and Shelter Swamp Creek, off north side of east/west trending road and ditch near east side access gate, lat. 34°36'51"N, long. 77°37'54"W; with *Rhynchospora thornei*, *R. latifolia*, *Oenothera fruticosa* var. *unguiculata*, *Andropogon glaucopsis*, *Dichanthelium acuminatum* var. *acuminatum*, *Symphyotrichum dumosum*, *Spiranthes vernalis*.

R.J. LeBlond 6958E 6 Jun 2013

Fig. 2. Holotype of *Scleria bellii* from Onlsow County, North Carolina (*LeBlond 6958*, NCU).

tional Forest, timber compartment 47, stand 03, with *Sporobolus curtissii, Muhlenbergia capillaris, Ctenium aromaticum, Rhexia alifanus, R. nashii, Helianthus angustifolius, Hypericum gymnanthum, Sabatia campanulata, Crotalaria purshiana, Eryngium yuccifolium, Bigelowia nudata* var. *nudata, Scleria pauciflora* var. *pauciflora*, 28 Jul 2012, *L. Lee s.n.* (NCU!); Francis Marion National Forest, in clumps on grassy, previously scraped ground at savanna edge, east side of Forest Service Rd 212, 640 m S of FSR 212F, 2.8 air mi E of downtown Homey Hill, 14 Sep 2012, *Nelson 31381* (USCH!). **Georgetown Co.:** ca. 3 mi NE of Campfield along US 701, mown roadside through former pine flatwoods, with *Dichromena latifolia, Aster dumosus, Chaptalia tomentosa, Plantago sparsiflora, Bigelowia nudata, Rhexia lutea, R. alifanus, Buchnera floridana, Rhynchospora pusilla, R. pinetorum*, 9 Jun 1994, *Sorrie 8031* (USCH!). **Jasper Co.:** common in pine-toothache grass savannah along S-169, 0.3 mile SW of jct. with U.S. 321, 11 Aug 1983, *Aulbach-Smith & Aulbach 2771* (USCH!). **York Co.:** Rock Hill Blackjacks Heritage Preserve, grassy open spots near powerline right of way, edge of rocky woods over Iredell soil, just W of rock quarry on S-245, SE Rock Hill, 26 Jun 1987, *Nelson 5734* (USCH!, CLEMS). **TEXAS. Harris Co.:** 22 Jun 1877, *Joor s.n.* (MO!); Houston, 1885, *Nealley s.n.* (NY!); a robust species among prairie grasses along Underwood St. at intersection with North St. in LaPorte, 6 Aug 1983, *Brown 6455* (BRIT!); sandy soil, coastal prairie W of Underwood St., 0.3 mi. N of Spencer Hwy, 26 May 1984, *Kessler & Brown 7467* (BRIT!, NY!).

DISCUSSION

Detailed morphometric analysis concentrated on the plants in eastern North Carolina; these were the only known extant populations until discovery of the Berkeley Co., South Carolina, populations in 2012. Other populations are known from one to a few herbarium specimens. Distinguishing characters established during the analysis of the eastern North Carolina plants were applied to the vegetative and floral structures (including at least one achene per sheet) of the populations represented only by herbarium specimens. Distinguishing characters include the full range of measurements and qualities (e.g., indument density and location) gathered from all specimens across the range of the species.

As with other *Scleria* species, the achene is critical in distinguishing *S. bellii*. Based on achene structure (Fig. 3), it appears to be most closely related to taxa in the informal *S. ciliata* complex, but also showing some morphological affinities with *S. oligantha* Michx. This treatment recognizes the following taxa in the *S. ciliata* complex: *S. ciliata* Michaux var. *ciliata*, *S. ciliata* var. *elliottii* (Chapm.) Fernald, *S. pauciflora* Muhl. ex Willd. var. *pauciflora*, and *S. pauciflora* var. *caroliniana* Alph. Wood. Other recent workers have recognized *S. curtissii* Britton in J.K. Small and *S. ciliata* var. *glabra* (Chapm.) Fairey within the *S. ciliata* complex. They also are discussed. Members of the *S. ciliata* complex together with *S. bellii* and *S. oligantha* are treated here as an informal group based on shared features of the hypogynium. *Scleria ciliata,* "sensu lato," is sometimes used for *S. ciliata* var. *ciliata* and *S. ciliata* var. *elliottii*, including synonyms.

The need to include *Scleria oligantha* in this study gradually evolved as *S. ciliata* sensu lato collections were examined. A few of the historical *S. bellii* collections had originally been identified as *S. oligantha*, and the structure of the *S. oligantha* hypogynium bears a strong resemblance to those of *S. bellii* and the *S. ciliata* complex. Because *S. oligantha* is readily distinguished from the other members of the group, the focus of analysis herein is on the morphological relationship of *S. bellii* with the more similar-appearing *S. ciliata* sensu lato. *Scleria oligantha* herbarium collections need to be examined for the presence of *S. bellii*.

Scleria bellii, S. oligantha, and members of the *S. ciliata* complex share distinctive features of the achene hypogynium, the structure that subtends the achene body in all *Scleria* species. This structure is rudimentary in some species, and in others can remain attached to the pedicel after detachment of the achene body. In the *Scleria bellii-ciliata-oligantha* group, the hypogynium consists of two parts visibile laterally: a broad and short basal rim, and three to nine protuberances (tubercles) located between the basal rim and the achene body (Fig. 3). The basal rim and tubercles provide important diagnostic characters for separating the taxa in this group. The rim is tan to dark brown and usually shiny. The tubercles are usually white or beige and surficially minutely papillose. Each papilla apex is rounded or pointed, with both apex types usually found on the same tubercle. The tubercle surface is similar to that of taxa in the *S. triglomerata* Michx. complex (*S. flaccida* Steud., *S. minor* W. Stone, *S. nitida* Willd.), which have an uninterrupted encircling hypogynium with a white papillose surface, and lack a laterally visible basal rim.

Structure of the hypogynium tubercles in the *Scleria bellii-ciliata-oligantha* group is variable. Individual tubercles can be isolated and distinct, or shallowly to deeply lobed, or confluent with an adjacent tubercle. Confluent tubercles are indicated by a suture. Tubercle variation often occurs on the same achene. Size of individual tubercles is useful in distinguishing *S. ciliata* sensu lato from *S. bellii* and *S. oligantha*. The *S. bellii*

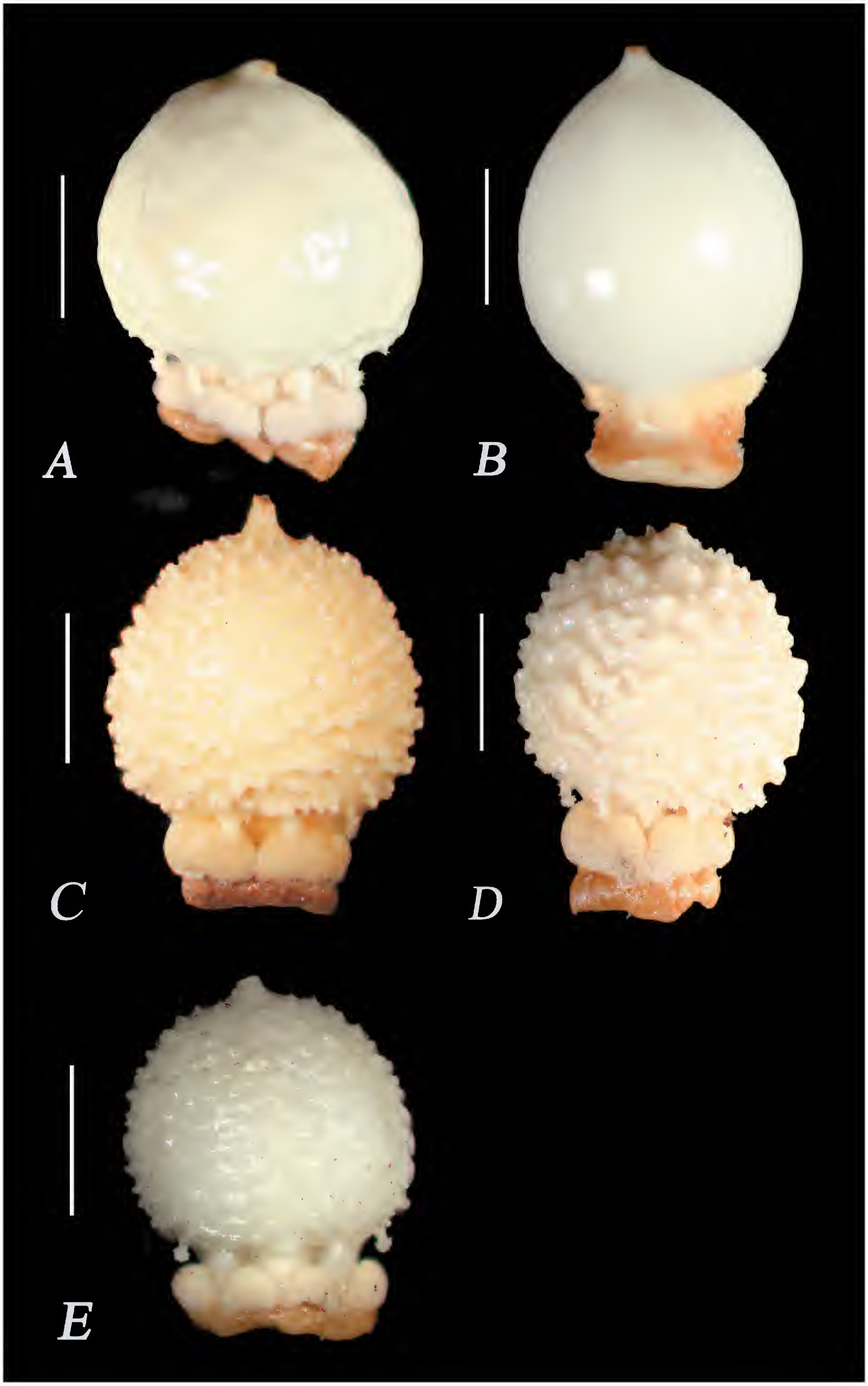

Fig. 3. Representative achenes of the *Scleria bellii-ciliata-oligantha* group. Note differences in surface ornamentation and tubercle number/size on the hypogynium. **A)** *S. bellii*, **B)** *S. oligantha*, **C)** *S. ciliata* var. *ciliata*, **D)** *S. ciliata* var. *elliottii*, and **E)** *S. pauciflora*. Scale bar = 1 mm.

hypogynium is comprised of (four-) six tubercles, compared with three sometimes lobed tubercles of *S. ciliata* sensu lato. Individual unlobed and nonconfluent tubercles in *S. bellii* average 0.3–0.5 mm wide, while those of *S. ciliata* sensu lato are 0.5–0.7 mm wide.

The achene surface also provides important diagnostic features for the *S. bellii-ciliata-oligantha* group. In all taxa, the mature achene is shiny and bony white (immature achenes are often darker and longitudinally sulcate). The surface texture in the *S. ciliata* complex is variable, ranging from papillose to transversely ridged to reticulate (including papillate ridging and reticulation). The mature achene body surface in *S. oligantha* is uniformly smooth.

It should be noted there are two very different structures on the achene in the *S. ciliata* complex that are described as papillate. The papillae on the achene body are readily visible at 10× and are about 0.1 mm in diameter or wider; their length can vary from < 0.1 mm to >0.2 mm. By comparison, tubercle papillae are minute and require stronger magnification to be seen.

It is achene body surface texture that most readily distinguishes *S. bellii*. Except for a few basal retrorse papillae, the body is epapillate and essentially smooth. A closer examination (10×) reveals broad low rises on the body surface, including occasional faint low transverse ridging. These characteristics are comparatively distinctive and occur throughout the range of the species. Achene dimensions, tubercle number, basal rim dimensions, leaf and bract widths, and herbage pubescence clearly distinguish *S. bellii*.

The surface sculpturing of the *Scleria bellii* achene body is unique among North American *Scleria*, and probably within *Scleria* as a whole. The few basally retrorse papillae and the character of the hypogynium, along with vegetative characteristics, are likely what led to historical identification of most collections as *S. ciliata* sensu lato (most frequently as *S. elliottii* or *S. ciliata* var. *elliottii*). Four collections were originally identified as *S. oligantha*.

Achene and hypogynium measurements alone can differentiate fairly well between *S. bellii, S. ciliata* var. *ciliata*, and *S. ciliata* var. *elliottii*. The *Scleria bellii* hypogynium basal rim is usually broader than that of *S. ciliata* sensu lato. Achene width, although strongly correlated with hypogynium width (R = 0.81), is also generally greater in *S. bellii* than in *S. ciliata* sensu lato (Fig. 4). Achene and hypogynium lengths in *S. bellii* overlap with measurements of both varieties of *S. ciliata*, although the *S. bellii* lengths have a narrower range. Kruskall-Wallis tests for one-way analysis of variance show that achene length, achene width, hypogynium length, and hypogynium width are each significantly different among the three taxa ($\alpha = 0.003$ with Bonferroni correction), although pairwise comparisons indicate that *S. belli* achene length and hypogynium length are not significantly different from *S. ciliata* var. *elliottii* and *S. ciliata* var. *ciliata*, respectively (Table 1). Of these metrics, achene width and hypogynium width are the strongest predictors, showing clear distinctions among the three taxa.

Special mention must be made of the collection of *Scleria bellii* from Jalisco, Mexico. Only one specimen has been seen (*Rzedowski 17703,* BRIT), and it contains a single achene. That achene has the overall dimensions, basal rim dimensions, and the six tubercles of typical mature *S. bellii* achenes, but lacks the body's basal papillae. The tubercles are also more distinctly separated than in typical specimens. The body is longitudinally sulcate, suggesting the achene may be immature. Culm and leaf dimensions and indument are the same as in typical *S. bellii*. More specimens need to be examined from this disjunct population.

The *Scleria bellii* inflorescence usually produces a terminal fascicle and one axillary fascicle (rarely two axillary, and rarely no axillary on what are likely late season culms). *Scleria ciliata* vars. *ciliata* and *elliottii* frequently produce culms with only terminal fascicles, as well as culms with both a terminal and one axillary fascicle. Terminal primary bracts are on average wider in *S. bellii*, and their cilia longer, as are the cilia of pistallate scale keels. Pistillate scales are glabrous in *S. bellii*, and glabrous to puberulent in *S. ciliata* sensu lato.

Vegetatively, *Scleria bellii* most closely resemble *S. ciliata* var. *elliottii*. On average, *S. bellii* culms are taller and the leaves wider. There are taxonomically important differences in culm and leaf indument. The *S. bellii* culm has stiff trichomes on the angles and primary veins, but is glabrous between the veins and angles. (The culm is sometimes puberulent between the angles and veins for 1-2 cm below the terminal fascicle.) The *S. ciliata* var. *elliottii* culm is puberulent throughout with hairs 0.1–0.4 mm long and often has stiff trichomes on

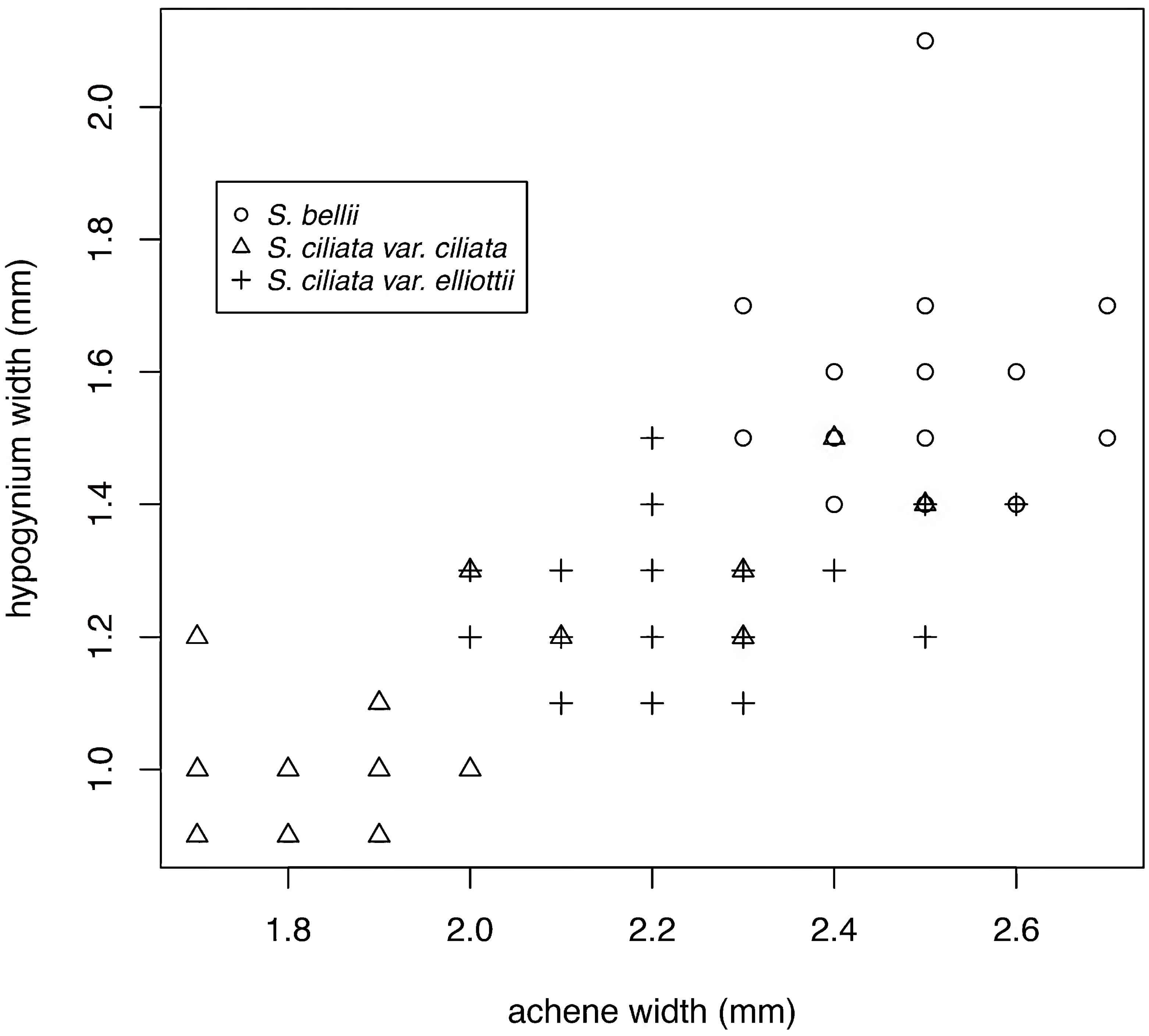

Fig. 4. Achene and hypogynium width variation in *S. bellii, S. ciliata* var. *ciliata,* and *S. ciliata* var. *elliottii.*

the angles and primary veins. Similar to the culm, the *S. bellii* leaf adaxial surface has stiff trichomes on the margins and primary veins, and is glabrous between the veins. In *S. ciliata* var. *elliottii*, the leaf adaxial surface is puberulent throughout with hairs 0.1–0.4 mm long, and often has stiff trichomes along the margins and primary veins.

Scleria oligantha readily separates from *S. bellii* and *S. ciliata* sensu lato by its eight or nine hypogynium tubercles, and achenes 2.5–4 mm long with uniformly smooth surfaces. The inflorescence is either a terminal fascicle, or terminal with one or two axillary fascicles. The axillary fascicles are borne on long filiform peduncles. The axillary fascicles in *S. bellii* and *S. ciliata* sensu lato are short to long-peduncled.

Plants in the *Scleria ciliata* complex with reticulate achenes have been recognized as *S. curtissii*, *S. ciliata* var. *curtissii* (Britton) J.W. Kessler, and *S. pauciflora* var. *curtissii* (Britton) Fairey (Small 1903; Fairey 1967; Kessler 1987). Sculpturing of the achene surface is quite variable in the complex, ranging from papillose to transversely ridged to reticulate (including papillate ridging and reticulation). Reticulation and transverse ridging sometimes occur in different areas on the same achene. Reticulate body surfaces can be found on achenes with 3 (*S. ciliata*) or 6 (*S. pauciflora*) tubercles, corresponding with the two varieties. Such variation argues against recognition of *curtissii* as distinct.

Table 1. Kruskall-Wallis chi-squared values from analysis of variance. p-values ≤ 0.005 are indicated in bold.

	Achene Length	Achene Width	Hypogynium Length	Hypogynium Width
Pairwise				
S. bellii/S. ciliata var. *ciliata*	**19.81**	**32.16**	0.0261	**33.87**
S. ciliata var. ciliata/S. ciliata var. *elliottii*	**16.03**	**15**	**9.46**	**15.58**
S. ciliata var. *elliottii/S. bellii*	1.57	**24.81**	**10.81**	**31.38**
All three taxa	**24.97**	**45.69**	**13.87**	**50.67**

Essentially glabrous *Scleria ciliata* plants have been recognized as *Scleria ciliata* var. *glabra*. In his protologue, Fairey (1967) describes the plants as "completely glabrous." An examination of specimens found that most plants identified as var. *glabra* have glabrous to glabrate culms and leaf blades. But sheaths, especially the lower, are puberulent, and terminal fascicle primary bracts are usually ciliate or scabrous-margined. There are many specimens identified as either var. *glabra*, var. *ciliata*, or *S. ciliata* sensu lato with few to some leaf margin and/or culm angle cilia. Thus, varietal assignment seems arbitrary. Glabrate plants are essentially restricted to the outer Coastal Plain, where they are sympatric with the more widespread ciliated plants. This difference in indument may be a response to environmental conditions, and in our opinion does not merit taxonomic recognition.

Herein, no attempt has been made to determine the validity of characters distinguishing *Scleria pauciflora* sensu lato within the *S. ciliata* complex. That work needs to be done. It is possible characters used here for other taxa in the group, including those of the hypogynium and herbage indument, may be of use. There were several specimens on which the hypogynium tubercle count and achene size were ambiguous.

Putative Origin.—The shared morphological features with members of the *S. ciliata-oligantha* group, especially in the achene, strongly suggest an evolutionary relationship. Regarding a hybrid origin, *S. ciliata* var. *elliottii* and *S. oligantha* appear to be the most likely candidates based on morphology, but several factors argue against this. So far, *S. bellii* has not been found with either of these taxa. *Scleria ciliata* var. *elliottii* and *S. oligantha* are sympatric over an extensive region, but *S. bellii* is restricted to a small portion of that region. *Scleria bellii* also occurs in the West Indies (Cuba), where *S. oligantha* is absent. Among the three, *S. bellii* has longer culms, wider leaves, and longer pubescence. Both *S. ciliata* var. *elliottii* and *S. oligantha* are often pubescent between the major veins on the leaf surface, while *S. bellii* is glabrous (rarely a few stiff trichomes between the veins abaxially). The absence of *S. ciliata* var. *elliottii* and *S. oligantha*—and sometimes all other *Scleria*—from known *S. bellii* sites strongly suggests an independently reproducing taxon.

The following key distinguishes the taxa in the *S. bellii-ciliata-oligantha* group. Within its range, the group is distinguished from all other *Scleria* by a hypogynium consisting of a basal rim subtending a series of three to nine tubercles. Characters used to distinguish *S. bellii* from *S. ciliata* varieties *ciliata* and *elliottii* are also shown in Table 2.

1. Tubercles 8 or 9; mature achene 2.5–4 mm long, the surface uniformly smooth; inflorescence axillary fascicles, when present, on elongate filiform peduncles ____ **S. oligantha**

1. Tubercles 3 or 6; mature achene 1–3.5 mm long, the surface either smoothish with broad low rises, or variously densely papillose, transversely ridged, or reticulate; when present, inflorescence axillary fascicles short to long-peduncled.

  2. Hypogynium with (5–)6 tubercles; achene 1–2.5 mm long, the body papillate or reticulate-roughened; leaves 1–2.5 mm wide.

    3. Plants glabrous to hairy, but not villous-ciliate, the hairs to 0.4 m m long ____ **S. pauciflora** var. **pauciflora**

    3. Plants villous-ciliate with spreading hairs 0.5–1 mm long ____ **S. pauciflora** var. **caroliniana**

  2. Hypogynium with 3 to 6 tubercles; if more than 3 tubercles, then achene 2.5–3.2(–3.4) mm long, the body smoothish with low broad rises, and leaves (2.5–)3–7 mm wide.

    4. Achene body smoothish with broad low rises, epapillate except for a few retrorse papillae at the very base, sometimes with faint transverse ridging; achene including hypogynium 2.5–3.2(–3.4) mm long, 2.3–2.7 mm wide; hypogynium basal rim 1.4–1.8(–2.1) mm wide, 0.1–0.2(–0.3) mm long; tubercles (4–)6, individual unlobed tubercles 0.3–0.5 mm wide; longer pistillate scale keel cilia 0.5–1.0 mm, the scale surface glabrous; terminal

Table 2. Key characters used to distinguish *Scleria bellii*, *S. ciliata* var. *ciliata*, and *S. ciliata* var. *elliottii*.

characters	*S. bellii*	*S. ciliata var. elliottii*	*S. ciliata var. ciliata*
achene body surface	smoothish with broad low rises, epapillate except at base, sometimes with a faint transverse ridge	papillose throughout, sometimes also/or transversely ridged and/or reticulate	papillose throughout, sometimes also/or transversely ridged and/or reticulate
full achene length (mm)	2.5–3.2(–3.4)	2.3–3.1(–3.3)	2.0–3.2(–3.5)
achene body width (mm)	2.3–2.7	2.0–2.5(–2.6)	1.7–2.3(–2.5)
hypogynium basal rim width (mm)	1.4–1.8(–2.1)	1.1–1.4(–1.6)	(0.6–)0.8–1.3(–1.5)
hypogynium basal rim length (mm)	0.1–0.2(–0.3)	(0.1–)0.2–0.4(–0.5)	0.1–0.2(–0.3)
tubercle number	6 (rarely 3 deeply lobed)	3 (sometimes deeply lobed)	3 (sometimes deeply lobed)
tubercle width (mm)	0.3–0.5	0.5–0.7	0.5–0.7
longer pistillate scale keel cilia (mm)	0.5–1.0	(0.1–)0.2–0.5	(0–)0.1–0.5
maximum width primary terminal bract (mm)	2.0–4.9	1.2–4.1	0.4–2.2
longer cilia on primary terminal bract (mm)	1.1–2.2	0.7–1.1(–1.3)	(0–)0.1–0.7(–0.9)
axillary inflorescences	1(–2)	0–1	0–1
leaf blade width (mm)	(2.5–)3–7	(2.5–)3–6 mm	1–3(–3.5)
blade margins and primary veins	ciliate with stiff trichomes	ciliate with stiff trichomes, or puberulent	eciliate, ciliate, or puberulent
leaf surface	glabrous between primary veins (rarely a few stiff trichomes)	puberulent at least adaxially	glabrous or puberulent
culm height (cm)	40–100	(15–)30–70	(15–)25–70(–75)

fascicle primary bract 2.0–4.9 mm wide at widest point, its longer cilia 1.1–2.2 mm; inflorescence a terminal and (0–)1(–2) axillary fascicles; leaf blades (2.5–)3–7 mm wide, with stiff hairs on margins and primary veins, rarely with a few stiff hairs between veins on abaxial surface, lacking fine puberulent hairs; culm height 40–100 cm __________ **S. bellii**

4. Achene body papillose throughout, sometimes also transversely ridged or reticulate (infrequently papillae absent in reticulate achenes); achene including hypogynium 2.0–3.3(–3.5) mm long, 1.7–2.4(–2.6) mm wide; hypogynium basal rim (0.6–)0.8–1.4(–1.6) mm wide, 0.1–0.4(–0.5) mm long; tubercles 3, entire to deeply lobed, the unlobed tubercles 0.5–0.7(–0.9) mm wide; longer pistillate scale keel cilia 0–0.5 mm, the scale surface glabrous or puberulent; terminal fascicle primary bract 0.4–4.1 mm wide at widest point, its longer cilia (0–)0.1–1.1(–1.3) mm; inflorescence a terminal and 0–1 axillary fascicles; leaf blades 1–6 mm wide, glabrous to ciliate on margins and primary veins, to puberulent with fine hairs over entire surface, especially adaxially; culm height 15–75 cm.

    5. Leaf blades (2.5–)3–6 mm wide, at least some adaxial surfaces puberulent throughout, often with stiff hairs on margins and primary veins; terminal fascicle primary bract 1.2–4.1 mm wide at widest point, its longer cilia 0.7–1.1(–1.3) mm; hypogynium basal rim 1.1–1.4(–1.6) mm wide, (0.1–)0.2–0.4(–0.5) mm long __________ **S. ciliata** var. **elliottii**

    5. Leaf blades 1–3(–3.5) mm wide, adaxial surface glabrous and eciliate, or glabrous and ciliate on margins, or puberulent and ciliate; terminal fascicle primary bract 0.4–2.2 mm wide at widest point, its longer cilia (0–)0.1–0.7(–0.9) mm long; hypogynium basal rim (0.6–)0.8–1.3(–1.5) mm wide, 0.1–0.2(–0.3) mm long ______ **S. ciliata** var. **ciliata**

DISTRIBUTION AND HABITAT

Although widespread, *S. bellii* populations are scattered to disjunct (Fig. 1). The population in Jalisco, Mexico, is about 1,300 kilometers (800 miles) from the next nearest population, in Harris Co., Texas. The populations in western Louisiana are about 800 kilometers (500 miles) disjunct from the population in Wakulla Co., Florida. In the U.S., 12 of the 14 known populations are on or near the outer portion of the Atlantic and Gulf Coastal Plain. It is possible the species was more common when sea level was lower, with a rising sea segmenting distribution. The other two U.S. populations are in the Piedmont of North and South Carolina. This restricted distribution, along with what is known of soil characteristics, suggest adaptation to restricted habitats (though they may have been more common historically). *Scleria bellii* is a species of conservation concern, and is ranked as imperiled globally (G1G2) by NatureServe (2015).

All of the known Coastal Plain sites occur on wet soils, primarily if not exclusively in pine savannas and coastal prairies. At the three North Carolina Coastal Plain sites where the soil properties are known, there is a calcareous influence even though the pH is usually acidic. These sites are fire-adapted wet acid pine and pine-cypress savannas characterized by a subterranean limestone layer usually too deep to raise pH above acidic levels, but close enough to contribute nutrients (LeBlond et al. 1994; LeBlond 2001). This natural community has been described as the Very Wet Loamy Pine Savanna (Schafale 2011). According to Schafale, "These communities are very rare with a limited and patchy geographic range. They often, maybe always, have inclusions where soils are high in calcium and have a higher pH (5.5 to 7.2), but the majority of their soil is similar to other pine savannas (pH 3.8–4.1)."

Associated species at the Berkeley Co., Georgetown Co., and Jasper Co. sites in South Carolina indicate a fire-adapted rich wet savanna habitat. Associates at the Georgetown Co. site include *Dichromena latifolia, Plantago sparsiflora,* and *Rhynchospora pinetorum*, species suggesting a calcareous influence.

The Wakulla Co., Florida, occurrence "could be described as a calcareously-influenced wet acid savanna or coastal prairie…Limestone is at or near the surface" (Anderson 2013). The two sites in Louisiana are described as coastal prairie (*Reid 6539*, LSU) or low prairie (*Palmer 7635*, MO, US). One of the collections from Harris Co., Texas, (*Kessler & Brown 3619*, BRIT, NY) refers to coastal prairie. The Reid collection from Calcasieu Parish, Louisiana, cites *Schizachyrium tenerum* and *S. scoparium* as dominants, suggesting that that site might be an occurrence of the West Gulf Coastal Plain Southern Calcareous Prairie (NatureServe 2015).

The two Piedmont sites, one each in North and South Carolina, occur on acid to neutral soils with a high ferro-magnesium content. Although the moisture regime at the Piedmont microsites is not known, the associated soil series is moderately well drained.

Habitat data for other sites are ambiguous, with "Clay land" for the Lake Co. site in Florida and "Replanted pine flatwoods" in Glynn Co., Georgia. There are no data for the site in west-central Cuba. The label for the collection from Jalisco, Mexico, describes the habitat as a *Pinus leiophylla* and *Quercus* spp. forest, which may be fire-adapted. It is not known whether the microsite is wet, mesic, or dry.

ACKNOWLEDGMENTS

We are grateful to Carol Ann McCormick, curator of the UNC-CH Herbarium (NCU), for managing the extensive gathering of collections. We are also indebted to the curators and staff of the many herbaria who sent those collections. Support and insight were also provided by colleagues Alan Weakley, Bruce Sorrie, and Brenda Wichmann. Appreciation is given to David J. Rosen and several other reviewers for their constructive contributions to the manuscript.

In this era of declining support for herbaria, at least in the U.S., it is important to note the critical role herbaria played in our understanding of the distribution, ecology, morphology, and phenology of this new species. These data are critical in guiding research and population protection efforts.

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BOOK REVIEW

Emmet J. Judziewicz, Robert W. Freckmann, Lynn G. Clark, & Merel R. Black. 2014. **Field Guide to Wisconsin Grasses.** (ISBN-978-0-299-30134-7, pbk). The University of Wisconsin Press, Madison. (**Orders:** http://uwpress.wisc.edu/order.html#individuals, 1-800-621-2736). $29.95 (eBook $24.95), 288 pp., 6" × 9".

This slender but information- and illustration-rich book is a winner. It is based on many years of effort and experience by a group of authors highly knowledgeable about grasses.

The volume covers 232 species of grasses in Wisconsin. With over 1,000 figures, it is no wonder that most species include several illustrations or photos, which typically include habitat shots, close-ups of spikelets and their constituent parts, inflorescences, and photos of growth habit. A tremendous amount of time, effort, and care clearly went into obtaining and selecting the illustrations and photos.

Most species are allotted one page, but others (e.g., *Elymus lanceolatus*, *Calamagrostis canadensis*) receive two. A county-wide distribution map for Wisconsin accompanies each species at the top. Beyond the treatments for species, the book includes chapters on *Morphology*, *Agrostology* (more generally and including prominent agrostologists of Wisconsin), *Grasses in Wisconsin Plant Communities*, and *Keys to the Grass Genera of Wisconsin*. Wrapping up the volume is the *Glossary, References, Illustration Credits,* and *Taxonomic Index*.

For the tax-paying public, from whom state-supported universities ultimately derive most of their funding, a volume like *Field Guide to Wisconsin Grasses* resonates more than the research that systematists carry out (myself included) on taxa from far-distant lands. Botanists in the state-supported schools should remember this reality and continue to publish relevant, useful information regionally.

The generally broad overlap in the distribution of grass species with Minnesota, Illinois, and Michigan suggests that this volume could be used productively in those states as well. *Field Guide to Wisconsin Grasses*, given its compact size, reasonable pricing, and quality of content, is an excellent model for future treatments.—*Neil Snow, PhD, T.M. Sperry Herbarium, Department of Biology, Pittsburg State University, Pittsburg, Kansas 66762, U.S.A.*

STYRAX PELTATUS (STYRACACEAE), A NEW SPECIES FROM OAXACA, MEXICO

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ABSTRACT

A new species of *Styrax* L. series *Valvatae* Perkins, **Styrax peltatus** from the Isthmus of Tehuantepec in southeastern Mexico, is described and illustrated. It is similar to the Mesoamerican species *S. conterminus* Donn. Sm., but differs in its shorter petioles, smaller chartaceous and nearly glabrous leaf blades with six to eight secondary veins on each side of the midvein, the presence of leaf domatia in the abaxial axils of the secondary veins, fewer-flowered inflorescences with more delicate rachises, and generally smaller flowers. The species is known only from the type collection, made from the Uxpanapa-Chimalapa Region of the Selva Zoque in far eastern Oaxaca.

Key Words: Endemic, Isthmus of Tehuantepec, IUCN Red List, Mexico, new species, Oaxaca, Selva Zoque, *Styrax*, Uxpanapa-Chimalapa Region

RESUMEN

Se describe e ilustra una especie nueva de *Styrax* L. series *Valvatae* Perkins, **Styrax peltatus** del istmo de Tehuantepec en el sureste de México. Es similar a la especie Mesoamericana *S. conterminus* Donn. Sm., pero difiere es sus pecíolos más cortos, láminas foliares más pequeñas cartáceas y casi glabras con seis a diez venas secundarias a cada lado del nervio principal, la presencia de domacios en las axilas abaxiales de las venas secundarias, inflorescencias con menos flores y raquis más delicados, y flores generalmente más pequeñas. La especie solo se conoce de la colección tipo, hecha en la región Uxpanapa-Chimalapa de la Selva Zoque en el extremo este de Oaxaca.

Styrax series *Valvatae* Perkins, with about 90 species, is endemic to the Neotropics and contains most of the Neotropical species of *Styrax*. The species of this clade are distinguished from other members of the genus by the combination of an evergreen habit, a fleshy to juicy indehiscent mesocarp, and an ellipsoid seed (Wallnöfer 1997; Fritsch 1999, 2001). Other distinguishing features are: bases of young shoots without stalked ferrugineous or fulvous stellate trichomes, unless these accompanied by a dense tomentum of trichomes of the same general color and type; a subcoriaceous corolla with valvate floral aestivation and straight sides; and a smooth (i.e., "non-crackled") seed coat (Fritsch 1999).

The species taxonomy of *Styrax* for western Texas, Mexico, and Mesoamerica, including that of the species of *S.* series *Valvatae* in these areas, has been recently revised (Fritsch 1997). After the revision, I examined a specimen of *S.* series *Valvatae* collected from the Uxpanapa-Chimalapa Region of southwestern Mexico that does not fit the key to species in Fritsch (1997) and whose combination of characters agrees with no other species in the genus. This species is described and illustrated here as new to science.

Styrax peltatus P.W. Fritsch, sp. nov. (**Figs. 1–2**). Type: MEXICO. Oaxaca. Mpio. San Miguel Chimalapa: Loma Larga, en la cabecera de la rama principal (S) del Río del Café al O de Cerro Guayabitas, ca. 40–45 km al N de San Pedro Tapanatepec, 16°44'N, 94°14'W, 1500 m, 6 Nov 1985 (fl), *Salomón Maya J. 2450* (holotype: MEXU not seen, digital image!; isotype: CAS!).

Haec species *Styrax conterminus* Donn. Sm. simillima, sed ab eo petiolis 7–10 mm long, laminis 7.7–9.8 × 2.1–2.5 cm chartaceis, paginae abaxialium laminae fere glabris, nervis laminae utroque costae latere 6–8, domatiis praesantibus, inflorescentiis 4–8-floris compositis, rhachidibus inflorescentiae 0.6–1 mm latis, floribus ubique parvioribus, calycibus 2.4–3 × 3.3–4 mm, squamis ad medium calycis 0.2–0.3 mm diametro differt.

Trees, evergreen, 8 m tall. Young branchlets and vegetative buds densely covered with overlapping light ferruginеous to tawny lacerate-margined peltate scales. Petioles 7–10 mm long; leaf blades narrowly oblong, 7.7–9.8 × 2.1–2.5 cm, 2.9–3.9 times as long as wide, chartaceous, adaxially olive brown and glabrous except for sparsely scattered lacerate-margined peltate scales on midvein, abaxially olive green and nearly glabrous except for

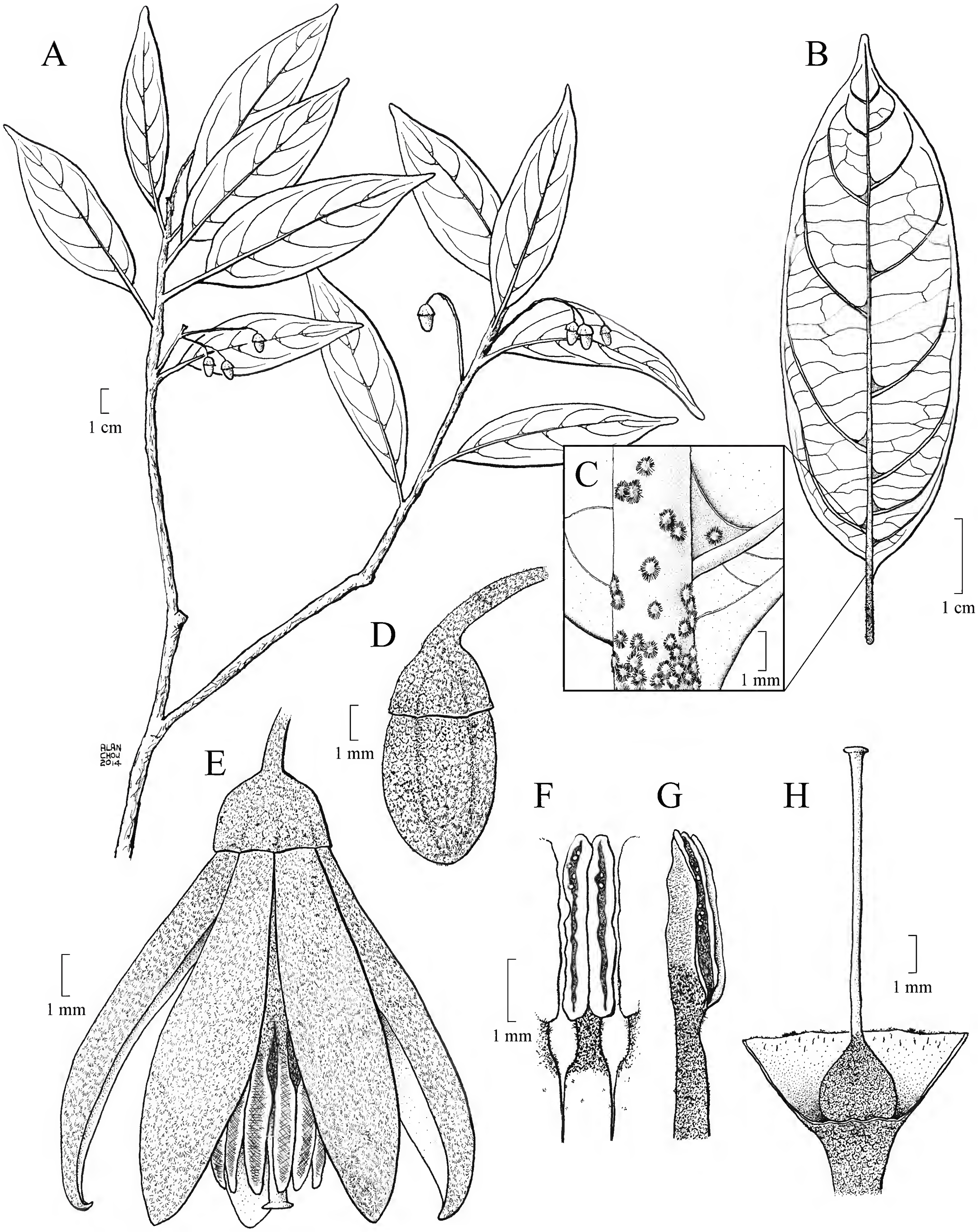

Fig. 1. *Styrax peltatus*. **A.** Branchlet with flower buds. **B.** Leaf, abaxial side. **C.** Close-up of abaxial side of leaf blade at base, showing lacerate-margined peltate scales and (shaded) one domatium. **D.** Pedicel and flower bud. **E.** Flower. **F.** Stamen, ventral view. Two adjacent stamens are incompletely drawn. **G.** Stamen, lateral view. **H.** Gynoecium and calyx, the latter cut away in front to show ovary. All drawn from the isotype *S. Maya J. 2450* (CAS).

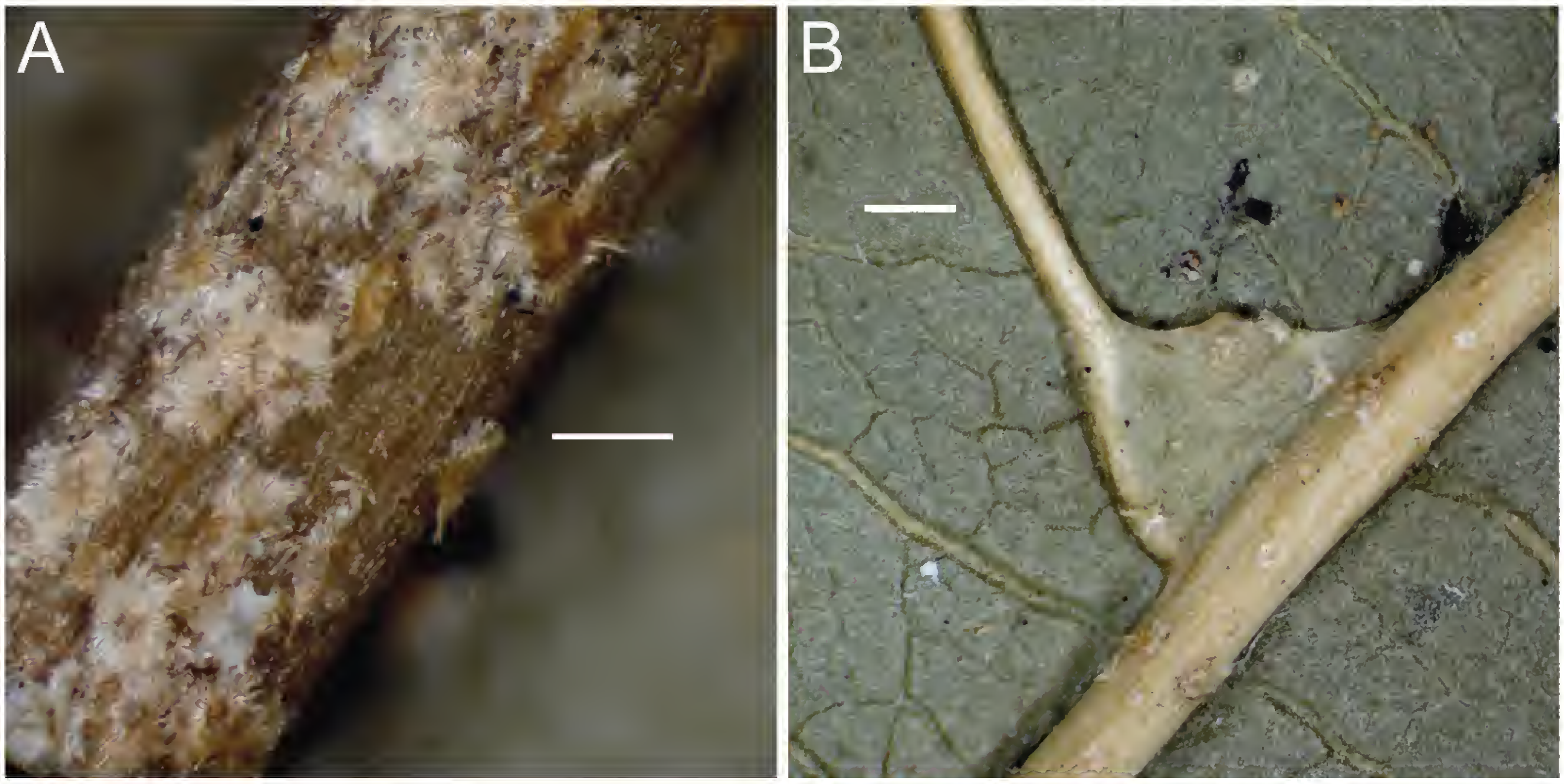

Fig. 2. *Styrax peltatus*, abaxial side of leaf blade. The leaf is oriented such that the proximal-to-distal direction is lower left to upper right. **A.** Midvein near base, showing lacerate-margined peltate scales. **B.** Surface, showing marsupiform domatium at the junction of the midvein and a secondary vein. Scale bars: A, 0.2 mm; B, 0.5 mm. From the isotype *S. Maya J. 2450* (CAS).

scattered lacerate-margined peltate scales on midvein and rarely on blade surface, scales 0.2–0.3 mm diam.; midvein raised abaxially, slightly depressed adaxially, secondary veins 6 to 8 on each side of midvein, often strongly upcurved near margin, tawny yellow, raised on both sides, tertiary veins generally perpendicular to midvein, slightly raised on both sides; base broadly cuneate to subrounded, margin entire, slightly revolute, apex abruptly acuminate; leaf domatia present abaxially in axils of secondary veins, marsupiform, deltoid, side along the midvein 1.6–2.2 mm long, glabrous or with sparsely scattered lacerate-margined peltate scales. Inflorescences axillary, racemose or paniculate, 2.5–4 cm long, 4- to 8-flowered, rachis 0.6–1 mm wide, rachis and pedicels covered with dense lacerate-margined peltate scales. Flowers hermaphroditic, ca. 10 mm long. Pedicels 5.5–7 mm long. Calyx obconic, 2.4–3 × 3.3–3.9 mm, densely covered with olive green to scattered pale orange peltate or lacerate-margined scales, margin truncate between the 5 minute teeth, margin toward inner (adaxial) side glandular, at mid-calyx the scales 0.2–0.3 mm diam., with 30–45 radiate arms. Corolla white, ca. 9 mm long, petals connate ca. 3 mm beyond the calyx margin; lobes 5, valvate in bud, thickened, ca. 6.5 × 1.2 mm, linear, abaxially covered with lacerate-margined peltate scales. Stamens 10; stamen tube diverging from corolla at ca. 2.5 mm, free portion ca. 3 mm long, dorsally covered with lacerate-margined peltate scales; distinct portion of filaments ca. 0.5–0.8 mm long, of equal width throughout, ventrally without auricles but bearing mixed radiate and lacerate-margined peltate scales at the somewhat incurved filament margins, more sparsely so on the inner surface, scales with arms to 0.18–0.24 mm long, the arms radiating from the central point in various directions, not primarily oriented parallel to the filament; anthers ca. 2.8–3.2 mm long, connectives glabrous; thecae linear, non-tapered, slightly to distinctly exceeding connective, with very sparsely scattered radiate scales on margins. Free portion of ovary rounded-pyramidal, densely covered with greenish white lacerate-margined peltate scales. Style filiform, ca. 7 mm long, glabrous; stigma ca. 0.3 mm wide. Fruit unknown.

Distribution, Habitat, and Phenology.—The new species is apparently endemic to the Atlantic slope rain forest of the Uxpanapa-Chimalapa Region, part of the Isthmus of Tehuantepec in southeastern Mexico. This region is in the Selva Zoque zone, known for its high species endemism (Wendt 1987, 1993). The type was collected in the Chimalapa part of the region, in far eastern Oaxaca near the border with Chiapas. It has been found only in the headwaters of the principal (south) branch of the Río del Cafe to the west of Cerro

Guayabitas, growing in pine-oak forest and in canyons in bosque mesófilo de montaña (montane mesophyll forest) of *Cedrela* P. Browne, *Liquidambar* L., and *Oecopetalum* Greenm. & C.H. Thomps. at 1500 m elevation. The only known collection was flowering in November.

Etymology.—The epithet refers to the peltate scales of this species, which occur nearly throughout the external surfaces of the plant, including the branchlets and vegetative buds, leaves, and inflorescences.

Conservation Status.—Because *Styrax peltatus* is known only from the type collection, we categorize this species as Data Deficient (DD; IUCN 2014). The label information denotes the species as abundant at the time of collection.

The morphological characters of *Styrax peltatus* are consistent with its placement among a phylogenetic grade of species within *S.* series *Valvatae.* These species all possess exclusively bisexual flowers (versus female and bisexual, i.e., plants gynodioecious), stamen filaments that are smooth ventrally (versus auriculate), trichomes with arms that radiate from the central point in various directions and typically do not exceed 0.5 mm long (versus primarily oriented parallel to the filament and are generally 0.8–2 mm long), and stamen thecae that are not tapered apically (versus tapered) and that equal or slightly exceed the connective (versus do not exceed the connective). The ten other species that comprise this grade (*S. austromexicanus* P.W. Fritsch, *S. conterminus* Donn. Sm., *S. gentryi* P.W. Fritsch, *S. incarnatus* P.W. Fritsch, *S. lanceolatus* P.W. Fritsch, *S. magnus* Lundell, *S. ochraceus* Urb., *S. radians* P.W. Fritsch, *S. ramirezii* Greenm., and *S. warscewiczii* Perkins) are together distributed in Mexico, Mesoamerica, and the Antilles (Fritsch 1999).

In the key to the species of *Styrax* of Mexico and Mesoamerica in Fritsch (1997), the first lead of couplet 4 (page 712) states "Abaxial laminar surface (and calyx) with vesture of peltate or lacerate-margined scales; scales at mid-calyx 0.72–0.44 mm diam.," and the other lead of the couplet states "Abaxial laminar surface with vesture of stellate hairs, or rarely radiate scales or nearly glabrous; scales at mid-calyx 0.05–0.33 mm diam., or else lacking." *Styrax peltatus* does not key out in this key because its calyx trichomes are lacerate-margined scales with a diameter at mid-calyx of 0.2–0.3 mm. If one followed the first lead, the new species would key to *S. conterminus* because of the shared characters of non-auriculate stamen filaments (versus strongly auriculate in *S. peruvianus* Zahlbr., the terminus of the alternative lead in couplet 5), leaves 2.8–2.9 times as long as wide (versus 2.0–3.1 times), and non-tapered anther thecae (versus tapered). *Styrax conterminus* is a Mesoamerican species of pine-oak and broad-leaved cloud forests that ranges from extreme southeastern Chiapas through Guatemala to northern El Salvador and western Honduras (Fritsch 1997). In addition to the differences in trichome diameter and geographic distribution, the new species is distinguishable from *S. conterminus* by the following characters: petioles 7–10 mm long (versus 13–25 mm); leaf blades 7.7–9.8 × 2.1–2.5 cm (versus 8.5–16.5 × 2.7–5.0 cm), chartaceous (versus thick-chartaceous), nearly glabrous on the abaxial surface (versus densely lepidote), secondary veins 6 to 8 on each side of midvein (versus 9 to 13), domatia present (versus absent); inflorescences 4- to 8-flowered (versus 4- to 20-flowered) with rachises 0.6–1 mm wide (versus 1.2–1.3 mm); calyces 2.4–3 × 3.3–4 mm (versus 3–4 × 4–5.5 mm); and generally smaller flowers.

Styrax peltatus could potentially be confused with *S. ramirezii* Greenm., a species also known to occur in the Uxpanapa-Chimalapa region (e.g., *S. Maya J. 3102*, CAS), because of the leaf and calyx vestiture in *S. ramirezii* that occasionally consists of scales. In this region, however, the abaxial leaf surfaces in plants of *S. ramirezii* are consistently covered by at least a thin tomentum, whereas in those of *S. peltatus* this surface is nearly glabrous. The leaves of the latter are also generally smaller, and the domatia are much larger (domatia are usually entirely lacking in *S. ramirezii*). Moreover, in *S. ramirezii* the calyx trichomes (and often those of the branchlets and leaves) are either stellate hairs, or radiate scales with the distal part of the arms often distinct, whereas in *S. peltatus* they are lacerate-margined peltate scales.

The only other species of *Styrax* from Mexico (and Mesoamerica) to be described after the revision of Fritsch (1997) is *S. uxpanapensis* P.W. Fritsch, also apparently endemic to the Uxpanapa-Chimalapa Region. It is easily distinguished from *S. peltatus* by a vestiture of stellate trichomes (versus scales) on most parts of the plant (e.g., branchlet, vegetative bud, leaf, inflorescence rachis, and calyx), and also by larger leaves 13–21.5 × 5.4–8.2 cm (versus 7.7–9.8 × 2.1–2.5 cm) and prominently auriculate stamen filaments (versus non-auriculate).

Styrax uxpanapensis is also distributed farther north than *S. peltatus*, i.e., in Oaxaca and Veracruz near the border shared between these states, and occurs at lower elevations (225–250 m versus 1500 m; Fritsch 2005).

ACKNOWLEDGMENTS

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BOOK REVIEW

H.C.F. Hopkins, Y. Pillon, & R. Hoogland. 2014. **Cunoniaceae: Flore de la Nouvelle-Calédonie. Vol. 26.** (ISBN: 978-2-85653-764-0, pbk). Publications scinetifiques du Muséum, IRD Éditions. Case postale 41, MNHN, 57 rue Cuvier, F-75231 Paris cedex 05, FRANCE. (**Orders:** diff.pub@mnhn.fr, 01-40-79-48-05). €59.00, 456 pp., 520 b/w illustrations & color photos, 25.5 cm × 16.5 cm.

Commencing with Volume 26, Cunoniaceae, the *Flore de la Nouvelle-Calédonie* has undergone a complete overhaul in presentation and style. I applaud the changes without hesitation, which are too numerous to fully enumerate.

The covers are of stiffer cardboard compared to earlier volumes and now are in color. In fact, color images are abundant in this volume of Cunoniaceae, which included treatments authored in parts by Jason C. Bradford, Gordon McPherson, Porter P. Lowry II, Bruno Fogliani, and Gildas Gâteblé.

It is entirely in French, apart from English translations for keys to genera, keys to genera using vegetative characters (to be used in conjunction with the illustrations), and keys to the species within genera. Seven genera are treated, which are easily located by colored bands (one per genus) on the outer margins of the page.

The volume covers 7 genera and 91 species, the richest being *Pancheria* and *Cunonia*. The distribution maps (one per species) now highlight the extensive ultramafic areas in color, unlike maps used in previous volumes. Cunoniaceae is a photogenic family, and numerous color photos and black and white illustrations (all of them excellent) occur throughout.

The family introduction is thorough and includes illustrations of key diagnostic characters (leaves, stipules, inflorescence structure, and fruits), separate comparative tables for reproductive and vegetative characters among the genera, and a table summarizing species number per genus and their distribution across ultramafic, non-ultramafic, and maqueé substrates. Also included are sections on reproductive biology, dispersal types, and chemical properties. Additional material is provided regarding the methodology underlying the taxonomic treatments.

Each species has iconic summaries at the top of whether it occurs on ultramafic and/or non-ultramafic rocks, its endemism status (all of them it appears), and its provisional IUCN conservation status. To reiterate, excellent line drawings and color photos abound. In some cases tabular comparisons are provided for morphologically similar species (e.g., in *Pancheria* and *Weinmannia*).

One new species, *Codia xerophila* Pillion, H.C. Hopkins & Gâteblé, is treated. A list of material examined by genus will be greatly appreciated by collections managers.

Reaching beyond taxonomy, the introduction also covers traditional medicinal uses, pharmacological and cosmetic uses, ornamental potential and uses, forestry and restoration applications, and information on seed germination and asexual reproduction *in vitro.*

My one minor complaint is that the font size on the "quick key to the species of *Cunonia*" is quite small. Aside from this, however, the authors and editors of Cunoniaceae have created a higher standard for future volumes of the *Flore.—Neil Snow, PhD, T.M. Sperry Herbarium, Pittsburg State University, Pittsburg, Kansas, 66762 U.S.A.*

NUEVAS ESPECIES DE *MACHERIUM* (LEGUMINOSAE: PAPILIONOIDEAE: DALBERGIAE) EN MÉXICO Y CENTROAMÉRICA

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RESUMEN

Se describen e ilustran cinco especies nuevas de *Machaerium* para México y Centroamérica. Asimismo, se discuten sus afinidades taxonómicas con otras especies.

Palabras Clave: Leguminosae, *Machaerium*, especies nuevas, México

ABSTRACT

Five new species of *Machaerium* from Mexico and Central America are described and illustrated, and their taxonomic affinities to other species are discussed.

Key Words: Leguminosae, *Machaerium*, new species, Mexico

INTRODUCCIÓN

Durante la preparación del manuscrito del tratamiento del género *Machaerium* para la *Flora Mesoamericana*, se examinaron las colectas de la región depositadas en los herbarios Nacional de México (MEXU), California Academy of Sciences (CAS), Missouri Botanical Garden (MO), New York Botanical Garden (NY) y Field Museum of Natural History (F), Duddley Herbarium (DS), Lundell Herbarium (LL) y material recientemente colectado en el sureste de México y todavía no distribuido. Además, se revisaron las descripciones recopiladas en los tratamientos existentes para las especies de la zona, como las de Pittier (1922), Standley y Steyermark (1946) y Rudd (1972, 1973, 1977, 1987) y el material tipo de la mayoría de las especies presentes en la zona hasta el momento de realizar este estudio. Con base en los ejemplares examinados y en el manuscrito de Linares y Rudd del género para la *Flora Mesoamericana*, se elaboró una clave dicótoma para todas las especies conocidas hasta el momento de México y Centroamérica. Como resultado del análisis del material disponible, se detectó la presencia de cinco nuevas para la ciencia, las que se proponen a continuación:

Machaerium ramosiae J. Linares, sp. nov. (**Fig. 1**). Tipo: MEXICO. Campeche: Municipio Calakmul, A 1.1 km al E de Conhuás lat 18°32'36"N, 89°54'46"O, 195 msnm Veg. Selva mediana subcaducifolia, Bejuco de flores blancas, 20 jul 2002, *D. Álvarez 1726* (holotipo: MEXU; isotipo: MEXU).

Vegetative haec species *Machaerio* semanii similis sed inflorescentiis brevioribus et robustioribus, partibus subglabris, 5 (exceptus 3) foliolis differt.

Bejucos grandes de hasta 20 m de largo, trepadores de otros árboles; ramitas fértiles grisáceas a blanquecinas, seríceas cuando jóvenes, glabras a muy esparcidamente pubescentes al madurar, con pelos subadpresos muy esparcidos, el indumento cuando presente café oscuro, estípulas de 1.5–2 mm de largo, triangulares a ligeramente falcadas, escariosas, deciduas; yemas vegetativas 0.9 mm, en las bases de las ramitas floríferas, ovoides; hojas 8–14 cm de largo; pulvino glabro o con unos cuantos pelos subadpresos luego glabrescente; pecíolo 2–2.5 cm de largo, glabro o glabrescente; raquis 2.5–4.5 cm de largo, terete, flexuoso, glabro o glabrescente; peciólulos 2–3 mm de largo, estrigosos a puberulentos cuando jóvenes, glabros o glabrescentes cuando maduros; folíolos 5, alternos; folíolos laterales 2.6–5 × (1.2–)1.5–2.2 cm, ovados, a veces oblicuamente ovados, la base

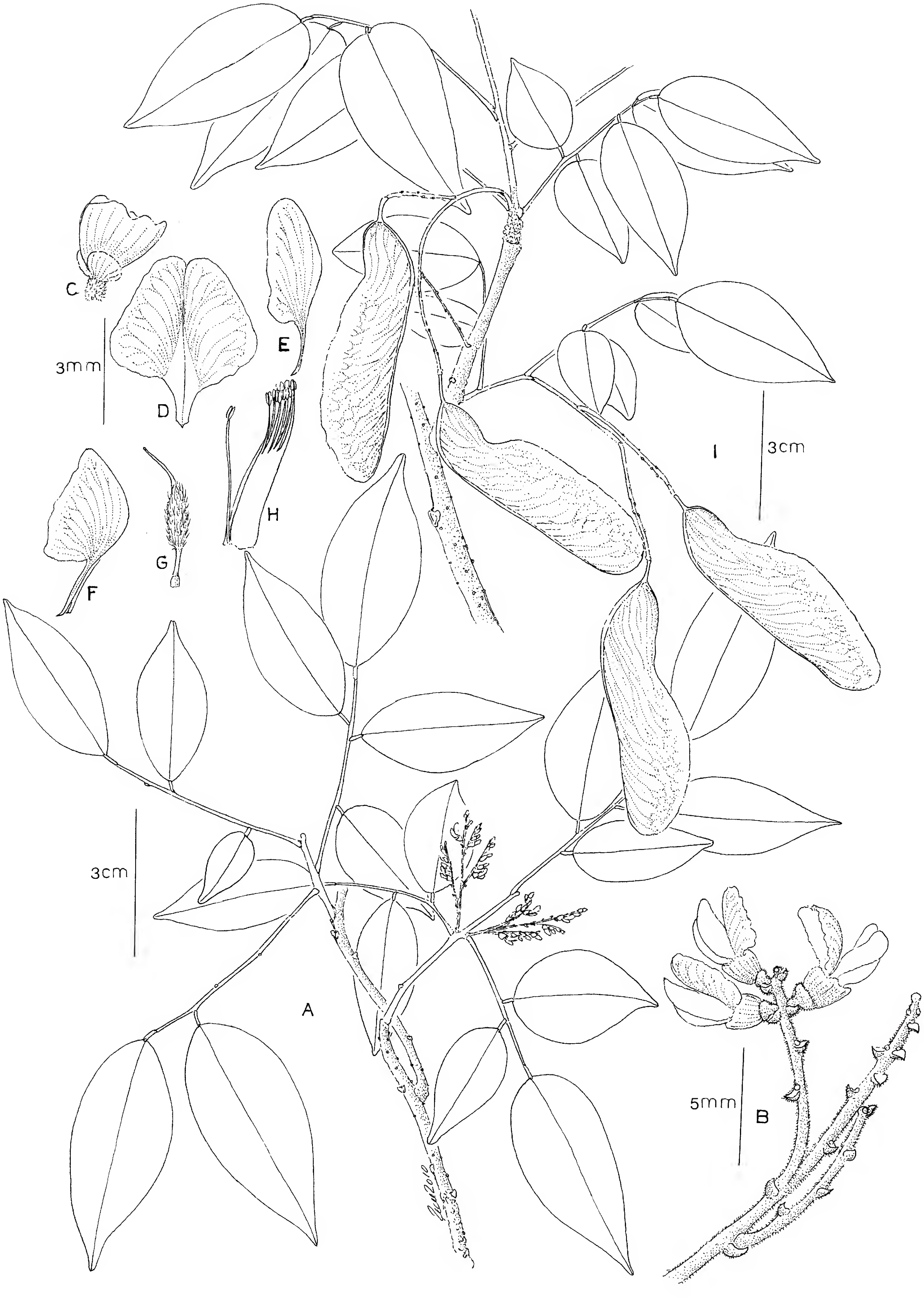

Fig. 1. *Macherium ramosiae* J. Linares. **A)** Rama floral. **B)** Inflorescencia. **C)** Cáliz. **D)** Estandarte. **E)** Ala. **F)** Quilla. **G)** Pistilo. **H)** Androceo. **I)** Rama con frutos, detalle de fruto. A–H tomados de *Alvarez 1726* (MEXU); I tomado de *Alvarez 6664* (MEXU).

obtusa a aguda, el ápice agudo a ligeramente acuminado, acumen 0.3 a 0.5 cm, el folíolo terminal 3.2–6.1 × 1.4–2.4(–3) cm, elíptico, base aguda o cuneada, ápice agudo a acuminado, todos los folíolos glabros o glabrescentes en el haz y en el envés cuando maduros, muy esparcidamente pubescentes cuando jóvenes, la nervadura central prominente por el envés; nervación broquidódroma, con nervaduras conspicuas entre las nervaduras secundarias; nervaduras terciarias reticuladas y notorias por el haz y envés. Inflorescencias axilares y terminales en ramitas del año de crecimiento, 1.5–3.5 cm de largo, muy cortamente pedunculadas el pedúnculo de 0.5–3.5 mm de largo, paniculadas, pedúnculo y raquis seríceos o velutinos, la pubescencia de tricomas café a café dorado, brácteas de las inflorescencias cuculiformes a cimbiformes, sésiles de 1–2 × 0.5–1 mm, papiráceas, seríceas, ciliadas en los bordes; Flores ca. 6.2 mm de largo, pediceladas, el pedicelo 0.5 mm de largo, las brácteolas 0.4 × 0.4 mm, deltoides cuando aplanadas, adpresas al cáliz, cuculiformes; cáliz 2.5 × 2.3 mm, campanulado, conspicuamente nervado, las nervaduras prominentes, esparcidamente pubescente, lobos adaxiales 0.3 × 0.5 mm, deltoides, los lobos laterales 0.2–0.4 × 0.4–0.5 mm, el abaxial 0.4 × 0.6 mm, triangular. El estandarte de 5 × 4 mm, incluyendo la uña de 1 × 1.8 mm, deltoide, la lámina del estandarte deltoide, pelosa en la parte adaxial, alas 7 × 2 mm (incluyendo la uña de 2 mm), lámina 5 × 2 mm, oblonga, casi glabra, quillas 5.5 × 1.5–1.7 mm, (incluyendo la uña de 1.5 a 1.8 mm), la lámina 2.5 ×1.5–1.7 mm, diminutamente pelosa hacia el lado abaxial, los estambres 10, diadelfos, el adaxial separado y los restantes unidos, 4.5–6 mm de largo, unidos en los 2.5 mm basales, anteras 0.2 × 0.3 mm, ovoides, disco nectarífero 1 × 0.5 mm, tubular, pistilo 5–5.5 mm de largo, pie 1.5 mm de largo, estilo 1.5 mm de largo, cuerpo 2–2.5 × 1 mm, peloso, el pedicelo y el estilo glabros. Frutos 6.5–7 × 1.7 cm, sigmoides, a veces doblándose casi en angulo recto a la altura de la camara seminífera, estípite 4–7 mm de largo, cámara seminífera 2 cm × 1.2 cm, ala 4.5–5 × 1.6–1.7 cm, margen adaxial marcadamente convexo, el abaxial ligeramente achatado, la nervación del fruto prominente. Semillas maduras no vistas.

Distribución, hábitat y fenología.—Conocida hasta ahora sólo de la región de Calakmul en Campeche, en selva mediana subperennifolia, selva baja subcaducifolia, selva mediana caducifolia y selva mediana subcaducifolia o vegetacion perturbada [datos tomados de las etiquetas] derivada de éstas entre 150 y 250 msnm.

Etimologia.—El nombre específico honra a la botánica mexicana Clara Hilda Ramos (1941–), dedicada estudiosa de la flora del sureste mexicano.

Florece en julio y fructifica probablemente de noviembre a diciembre.

Material examinado.—**MEXICO. Campeche:** Mpio. Champotón, 18°31'40"N, 089°54'10"O, 150 msnm, selva mediana subperennifolia, secundaria, ruderal, suelo negro. Arbusto perenne, 4 m, regular, flor blanca, 4 abr 1995, *C. Gutiérrez B. 4637*(MEXU). Mpio. Calakmul, A 1.1 km al NEE de Conhuás, camino a la Zona Arqueológica Nadzcaan, 18°32'35"N, 89°54'45"O, 193 msnm. Veg. Selva mediana caducifolia, bejuco leñoso con frutos verdes, 20 ago 2002, *D. Álvarez, et al. 1873*(MEXU); A 5 km al NE de Calakmul. 18°8'35"N 89°47'2"O, 230 msnm. Veg. Selva baja subcaducifolia, arbusto voluble con fruto, 9 dic 1998, *E. Martínez et S. Ramírez A. 31647* (MEXU); 3 km al Sur de Conhuas, 18°31'30"N, 089°56'00"O, 150 msnm, suelo somero, hierba perenne, 5 m, regular, fruto verde, 5 jul 1995, *C. Gutiérrez 4462* (MEXU); A 3.35 km al SE del poblado de Conhuas, camino a Zona Arquelógica de Calakmul lat 18°31'0"N, 89°54'8"O, 165 msnm, Veg. Secundaria, bejuco, flores amarillas y látex blanco, 30 sep 2003, *D. Álvarez y C. Jiménez 6664* (MEXU).

Discusión.—Vegetativamente esta especie es similar a *Machaerium seemannii*, pero se distingue de ella por las inflorescencias las cuales son más cortas y robustas en *M. semmannii*. Asimismo, *M. seemmanii* tiene inflorescencias con raquis, flores y frutos seríceos a velutinos, versus las partes casi glabras de la especie nueva. Por otra parte *M. semmannii* tiene de 9 a 13 folíolos, versus los 5 (excepcionalmente 3) de la nueva especie.

Machaerium excavatum J. Linares, sp. nov. (**Fig. 2**). Tipo: COSTA RICA. San José: Mpio. San Isidro del General, Basin of El General, 675–900 m, Feb 1940, *A.F. Skutch 4705* (holotipo: NY; isotipos: NY, US).

Haec species foliolis magnis et grande caudatis atque habitu volubili giganteo, fructibus incisura notabili ad altitudinem loci seminalis ad partem adaxialem, sicut *Machaerium darienense*, distinguitur; a *Machaerio darienensi* foliolorum numero, forma et magnitudine atque cavitatis magnitudine margine abaxiali differt.

Bejucos gigantes de hasta 20 m de largo, trepadores en otros árboles, a veces reportado como arbolito de 3–5 m, dentro del sotobosque; ramitas floríferas blanquecinas a grisáceas, conspicuamente lenticeladas, glabras; hojas con estípulas de 5–8 × 2–3 mm, glabras, triangulares, cocleadas, algo falcadas, papiráceas o pajizas, persis-

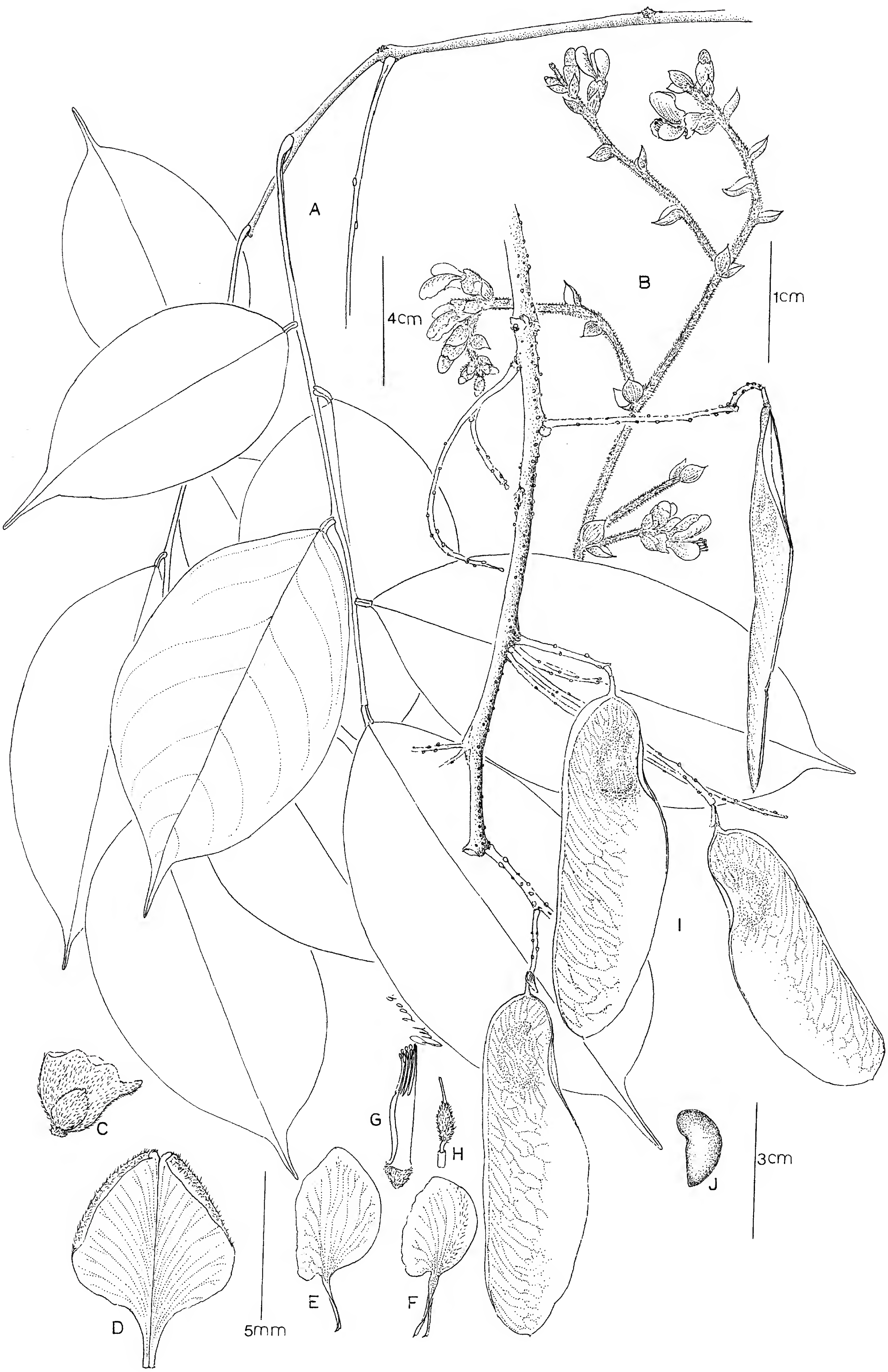

Fig. 2. *Macherium excavatum* J. Linares. **A)** Rama con hojas. **B)** Inflorescencia. **C)** Cáliz y brácteolas. **D)** Estandarte. **E)** Ala. **F)** Quilla. **G)** Androceo. **H)** Gineceo. **I)** Rama con frutos. **J)** Semilla. A tomado de *Croat 14994* (US); B–H tomados de *Skutch 4316* (US); I detalle de fruto. A–H tomados de *Alvarez 1726* (MEXU); I–J tomado de *Skutch 4705* (US).

tentes; yemas vegetativas axilares, presentes sólo en ramas estériles, ovoides, de 2–7 × 1–2.5 mm, cubiertas de catáfilas imbricadas; hojas (17)22–30 cm de largo (probablemente mucho más grandes), pulvino glabro o glabrescente, pecíolo (2)4–6 cm de largo, glabro; raquis 5–10.5 cm de largo, terete, recto, glabro o glabrescente; peciolulos 2–5 mm de largo, glabros o glabrescentes; folíolos 5, alternos, folíolos laterales 7–15 × 3–6.2 cm, ampliamente elípticos a obovados, la base aguda a obtusa, el margen liso y ápice caudado, folíolo terminal de 10–15 × 4–9 cm, ampliamente elíptico a obovados, la base atenuada a cuneada, el margen liso y el ápice caudado, el acumen en todos los folíolos 1–3.5 × 0.2–1 cm, todos los folíolos glabros a estrigulosos en el haz y en el envés (muy diminutamente), la nervadura central prominente por el envés; nervación broquidódroma, con nervaduras conspicuas entre las nervaduras secundarias; nervaduras terciarias reticuladas y muy notorias por el haz y envés. Inflorescencias axilares paniculadas en ramitas del año y en las partes desnudas adyacentes, 8–12 cm de largo, pedúnculo de 2 mm de largo, brácteas de la inflorescencia 2.5–3 × 1.5–2 mm, cuculadas a cóncavas, papiráceas, el pedúnculo y el raquis estrigoso a seríceo, la pubescencia de tricomas café a café-dorado, brácteas de las inflorescencias; Flores 8–9 mm de largo, pediceladas, el pedicelo 0.6 mm de largo, las bractéolas 1.9 × 2 mm(2.4 × 2.3 mm ya abiertas), deltoides cuando aplanadas, algo cuculiformes, adpresas al cáliz; cáliz 2.3–3.2 × 3 mm, campanulado, marcadamente nervado, estrigoso a seríceo conspicuamente nervados, las nervaduras prominentes, los lobos del cáliz irregulares, los adaxiales 2 × 0.8 mm, los laterales 0.9 × 0.9 mm y el abaxial 0.8 × 0.7 mm, deltoides. El estandarte 6–8 × 6.2–6.5 mm, incluyendo la uña 2 × 2 mm, la lámina flabelada, con el ápice retuso, seríceo hacia la nervadura media por la cara adaxial; alas 7 × 3 mm (incluyendo la uña 2.5 mm de largo), lámina 4.9 × 3 mm, obovada, casi glabras, quillas 6 × 2.9 mm, (incluyendo la uña de 2 mm), la lámina 3.9–4 × 2.8–2.9 mm, auricular, serícea en la parte media y glabra hacia los bordes. Estambres 10, unidos todos, excepto por el lado adaxial, 5–7 mm de largo, con la parte unida 2.5–3 mm de largo, anteras 0.6 × 0.5 mm, ovadas, el disco nectarífero de 1.2 × 1 mm, urceolado a tubular; pistilo 5 × 1 mm, pie 2 mm de largo, estilo 1.2 mm de largo, cuerpo 1.7 × 1 mm, oblongo, seríceo, el pedicelo y el estilo glabros. Frutos 7.5–12 × 2–2.8 cm, cámara seminífera 1.8–3 × 1.8 cm, el ala 4.7–7 × 1.9–2.5 cm, ambas con nervaduras muy marcadas, frutos oblongos, el margen adaxial recto o casi recto y conspicuamente engrosado, el abaxial ligeramente sigmoide achatado y muy expandido a la altura de la cámara seminífera formando una cavidad de hasta 4 mm de ancho en la parte más ancha. Semillas maduras no vistas.

Distribución, hábitat y fenología.—Conocida hasta ahora sólo de la región sur de Costa Rica, del bosque lluvioso de Golfo Dulce y de San Isidro del General, en bosques premontanos de 10–1000 msnm.

Etimologia.—El epíteto específico alude a la depresión de la camara seminífera en el margen abaxial del fruto que distingue a esta especie.

Florece en junio y fructifica de enero a marzo.

Material examinado.—**COSTA RICA. San José:** Mpio. San Isidro del General, Basin of El General, alt. 675–900 m, Jun 1940, *A.F. Skutch 4954* (NY, US); Cantón Puriscal, Zapotón de Puriscal, Arbolito creciendo en un paredón a orillas del camino, inclinado, frutos abundantes de color verde-limón, 31 ene 1986, *N. Zamora et al. 1161* (CAS); San Martín, Camino a Parrita, 9°44'10"N, 84°24'50"O, 800 m, arbolito de 5 m × 13 cm de DAP, ubicado en paredón cercano a la carretera, frutos muy abundantes verde-amarillentos, 29 nov 1989, *Q. Jiménez et al. 750* (MEXU); vicinity of El General, 640 m, Riverside cliff, Jun 1939, *A.F. Skutch 4316* (US); cut over hills, ca. 8 km SW of San Isidro del General, 1000 m, small tree 3–5 m tall, in forest, 27 Jan 1965, *L.O. Williams et al. 28383* (NY, US). **Puntarenas. Sin Mpio.:** along N fork (known locally as "Quebrada Mona") of Quebrada Bonita, Carara reserve, 9°47'N, 84°36'O, 35–40 m, giant liana, hanging low along creek and in association with major treefall in primary forest, samaras light green with fine, darker veins (uniformly dark at base), 31 Aug 1985, *M.H. Grayum et al. 5952* (MEXU, MO), Reserva Biológica Carara Sector Quebrada Bonita, Sitio Sendero Valentín, 9°46'20"N, 84°36'35"O, 70 m, 11 ene 1990, *R. Zúñiga 75* (MEXU); Cantón (?), Lomas de Cerro Esquivel, entre Santiago de San Ramón y Macacona de Esparza. 10°02'55"N, 84°36'20"O, 300–500 m, bejuco trepador, frutos inmaduros verde-amarillo, 15 sep 1986, *G. Herrera et al. 3* (CAS, MEXU); Cantón Golfito, Península de Osa. Puerto Jiménez. Cabecera Corozal. 08°32'30"N, 83°18'30"O, 1–10 m, Bejuco, muy común. Frutos verdes, 4 feb 1995, *R. Aguilar 3745* (NY); entre Puerto Jiménez y Agujas, entre los Ríos Agujas y Terrones. 08°33'55"N, 83°23'20"O, 50 m, Arbusto–bejuco, frutos verdes, 19 oct 1994, *R. Aguilar y J. González 3614* (NY); Santo Domingo de Golfo Dulce, *Tonduz 7018*, Forêts de Santo Domingo de Golfo Dulce, mar 1896, *Tonduz 7242* (US).

Discusión.—Esta es una de las especies más distintivas, vegetativamente y resalta por sus folíolos de gran tamaño y grandemente caudados, así como su hábito de liana gigante. Sus frutos son muy característicos por tener una muesca muy notoria a la altura de la cámara seminal por el lado abaxial, característica sólo compartida por *M. darienense*. Se distingue de esta última especie por el número, forma y tamaño de los folíolos, asi como el tamaño de la cavidad en el margen abaxial.

Machaerium paucifoliolatum J. Linares, sp. nov. (**Fig. 3**). Tipo: NICARAGUA. Chontales: Municipio La Gateada (¿), ca. 4.5 km S of Hwy 7 (from ca. 3.6 km E of La Gateada) on road to Nueva Guinea, ca. 12°57'N, 85°45'O, ca. 200 m, cut-over tall wet forest, disturbed roadside and pastures with scattered individual trees and small remnant patches of forest, one seen, large woody vine, climbing to canopy of large tree and forming dense masses, corolla white except wings brown, 17 Jul 1977, *W.D. Stevens 2847* (holotipo: MEXU).

Vegetative haec species *Machaerio pittieri* similis, praeter 3 foliola, fructum angustiorem et saepe forte sigmoideum versus flexum in "L."

Bejucos grandes de hasta 20 m de alto, trepadores de otros árboles; ramitas fértiles grisáceas a blanquecinas, glabras, estriadas, lenticeladas, las del año anterior similares pero más blanquecinas. Estípulas de 1.6 × 1.2 mm, triangulares a ligeramente falcadas, prontamente deciduas; yemas vegetativas axilares 0.7–2 × 0.5–1.2 mm, ovoides, presentes en las hojas y en los ápices de las ramas, yemas seriales presentes y en zigzag; Hojas 7–17 cm de largo; pulvino glabro o con unos cuantos pelos subadpresos, glabrescente; pecíolo 2–3.5 cm de largo, glabro o glabrescente; raquis 1.1–2.5 cm de largo, terete, recto, glabro o glabrescente; peciólulos 2–3 mm de largo, glabros o muy esparcidamente pubescentes; folíolos 3, alternos; folíolos laterales 3–8 × 1.9–4.9 cm, ovados a anchamente elípticos, la base atenuada a obtusa, el ápice, acuminado o caudado, con un acumen de ca. 1.5 × 0.4 cm, el borde entero, sin pelos, el folíolo terminal 5–11 × 2.3–5 cm, elíptico, anchamente elíptico, ovado u obovado, base obtusa a aguda, ápice agudo a acuminado, todos los folíolos glabros o glabrescentes en el haz y en el envés, la nervadura central prominente por el envés; nervación broquidódroma, con nervaduras conspicuas entre las nervaduras secundarias; nervaduras terciarias reticuladas y notorias por el haz y envés, nervaduras secundarias 6–8 pares. Inflorescencias axilares y terminales en ramitas del año 1.5–3.5 cm de largo, muy cortamente pedunculadas el pedúnculo de 0.5–3.5 mm de largo, paniculadas, el pedúnculo y el raquis seríceo o velutino, la pubescencia de tricomas café a café-dorado, brácteas de las inflorescencias cuculiformes a cimbiformes, sésiles, 1–2 × 0.5–1 mm, papiráceas, seríceas, ciliadas en los bordes; flores 7 mm de largo, pediceladas, el pedicelo 0.5 mm de largo, las bractéolas 2.5 × 1.2 mm, extendidas (1.5 × 1.5 mm en posición normal), deltoides cuando aplanadas, algo cuculiformes, adpresas al cáliz; bractéolas 0.4–0.6 × 1–1.1 mm, cuculiformes; cáliz 3 × 2.5 mm, campanulado, conspicuamente nervados, las nervaduras prominentes, no llegan hasta el borde del cáliz, esparcidamente pubescente, lobos adaxiales 1.7 × 0.7 mm, deltoides, los tres restantes más pequeños 0.9 × 0.6 mm, deltoides. El estandarte 5.5 × 6 mm, incluyendo la uña 1.2 ×2 mm, deltoide, lámina del estandarte obcordada (cuando aplanada), serícea hacia el lado adaxial, alas 5.5 × 1.5 mm (incluyendo la uña 1.8 mm de largo), lámina 3.7 × 1.5 mm, oblonga, pelosas en la parte adaxial, quillas 5.5–5.8 × 2 mm (incluyendo la uña 2–2.2 mm de largo), la lámina 3.5–3.8 × 2 mm, oblonga, pelosa hacia el lado abaxial, corolas blancas con las alas café. Estambres 10, diadelfos, el adaxial separado y los restantes unidos, 4–5 mm de largo (incluyendo las anteras), filamentos lateralmente comprimidos (0.3 mm de ancho), anteras 0.3 × 0.3 mm, ovoides, disco nectarífero 0.6 × 0.4 mm, tubular, crenado, con 10 crestas. Pistilo 5.5 mm de largo, pie 1 mm de largo, estilo 1.2 mm de largo, cuerpo 3 × 1 mm, peloso, el pedicelo y el estilo glabros. Frutos 7–9 × 1.1–2 cm. sigmoides, a veces doblados casi en "L" a la altura de la cámara seminífera, cámara seminífera 2.5 × 0.9 cm, estípite 3–5 mm, alas 4.5–7 × 1.1–2 cm, acuminada, obtusa o redondeada, glabra, margen adaxial marcadamente convexo, el abaxial ligeramente achatado y canaliculado en la cámara seminífera, la nervación del fruto prominente. Semillas maduras no vistas.

Distribución, hábitat y fenología.—Conocida de selvas húmedas (SAP), pluvioselvas, bosques premontanos, de Honduras y Nicaragua donde crece en la vertiente Caribe y en Costa Rica donde crece en ambas vertiente oceánicas, florece en julio y fructifica en enero-marzo.

Etimologia.—El nombre específico alude al reducido número de folíolos característico de esta especie.

Material examinado.—**HONDURAS. Olancho:** Mpio. Santa María del Real, camino a represa del Río Real, Árbol 15m, 14°50'78"N 85°56'76[sic]"O, 550 m, 20 marzo 2006, *P.R. House et al. 3709* (MEXU). **NICARAGUA. Chontales:** Mpio. Cuapa, 0.8 km N of Cuapa, pasture fencerows, 340 m, tree collected along edge of woody area, fruits dark green, 12–15 m, 22 Jan 1978, *P.C. Vincelli 101* (MEXU); 3 km N of Cuapa, premontane moist forest, elev. 500 m. Small tree 7 m, 3 Sep 1977, *D. Neill 2501* (MEXU); ca. 2.8 km above (N of) Cuapa, ca. 12°17'N,

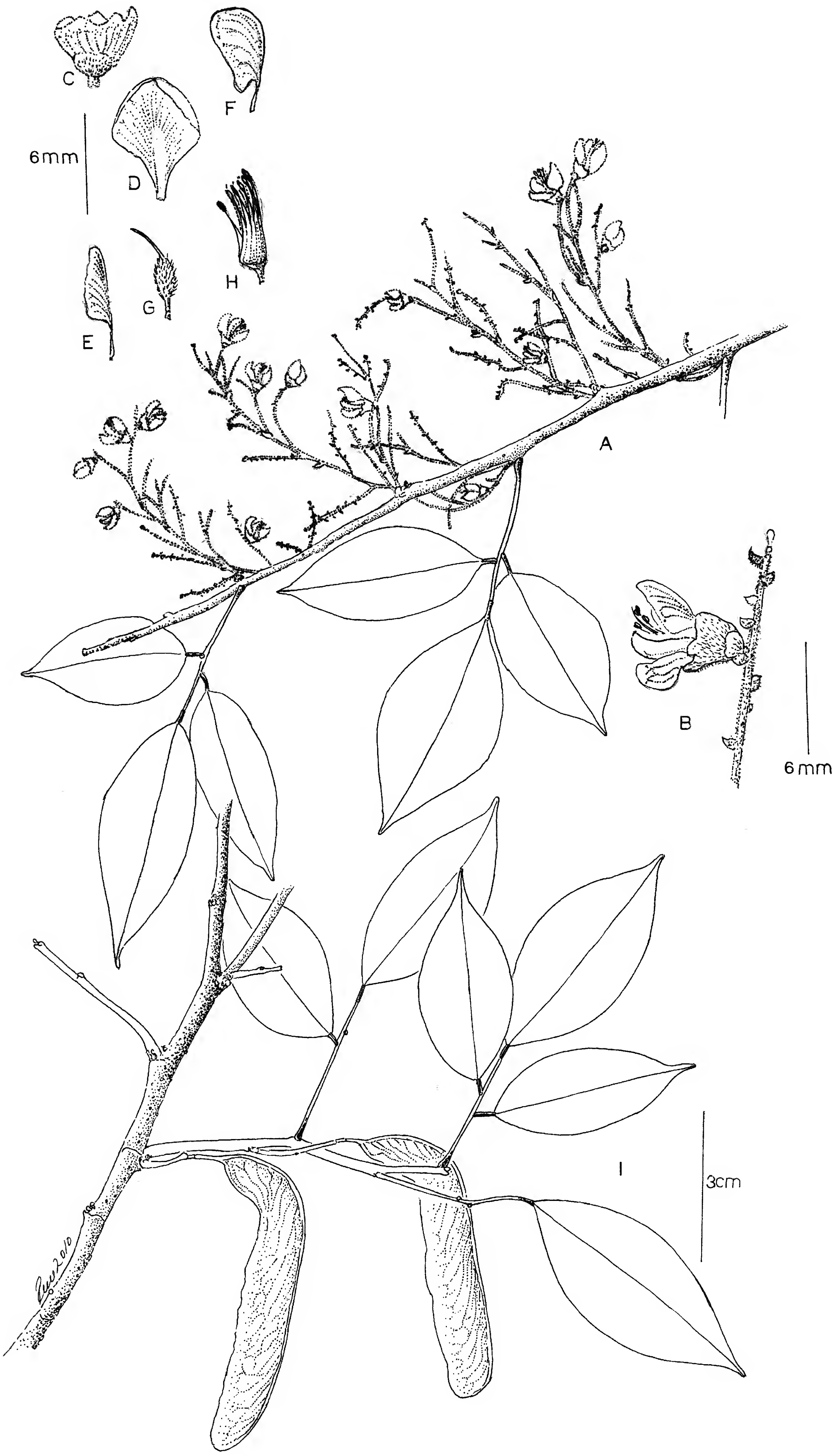

Fig. 3. *Macherium paucifoliolatum* J. Linares. **A)** Rama con hojas. **B)** Flor. **C)** Cáliz. **D)** Estandarte. **E)** Ala. **F)** Quilla. **G)** Androceo. **H)** Gineceo. **I)** Rama con frutos. A–H tomados de *Warren et al. 2847* (MEXU); I tomado de *Vincelli 101* (MEXU).

85°23'O, 400–500 m, roadside, pastures, disturbed evergreen forest on hillside, and along small stream, forest, large woody vine, climbing by thick tendrils, wing of fruit pale yellow-green, *W.D. Stevens 6055* (MEXU). **Matagalpa:** Mpio. Matagalpa, cut-over hills ca. 15 km NE of Matagalpa along Río Las Cañas, ± 700–800 m, 14 Jan 1965, *L.O.Williams et al. 27540* (DS, NY, US). **Nueva Segovia:** ca. k 233.5, ca. 6.2 km N of N, edge of Ocotal, Quebrada El Nancital, ca. 13°41'N, 86°24'O, 700–760 m, mixed evergreen and deciduous forest in quebrada, cut-over pine forest on slopes and ridge, large fallen tree along stream, leaves deep green, flowers white, fading to brown, *W.D. Stevens 3036* (MEXU). **COSTA RICA. Alajuela:** Cantón Los Chiles, R.N.V.S. Caño Negro, Llanura de Guatuso. Caño Negro, Playuelas. 10°54'50"N 84°46'05"O 40 m, arbusto escandente de 4 m, frutos con parte seminal o semífera, verde y el ala amarillo-verdoso, Es muy común en el lugar, 3 feb 1993, *K. Martínez et al. 54* (NY); Rio Chiquito, approx. 40 km Road to Upala, 800 m, *L.D. Gómez 18616* (MEXU). **Guanacaste:** Mpio. Santa Rosa, Camino del ICE de Santa Cruz a Vista de Mar, 900 m, bejuco de área en crecimiento secundario, flores aromáticas, café amarillento, 22–26 jul 1985, *L.D. Gómez et G. Herrera 23672* (CAS, MEXU,

Discusión.—Vegetativamente esta especie es similar a *Machaerium pittieri*, excepto que siempre presenta tres folíolos versus *M. pittieri* que siempre tiene cinco o más, además, el fruto es mas angosto y a menudo fuertemente sigmoide a doblado en "L."

Machaerium rubrinervum J. Linares, sp. nov. (**Fig. 4**). Tipo: COSTA RICA. PUNTARENAS: Cantón Osa, R.F. Golfo Dulce, Cuenca Térraba-Sierpe, Bahia Chal., La Parcela, 8°43'50"N 83°27'17"O, 150 m, bejuco leñoso, flores con el estandarte exteriormente pubescente, amarillo brillante, internamente morado oscuro, quilla verdosa-amarillenta, 1 ago 1996, *R. Aguilar 4635* (holotipo: NY).

Haec species insigniter distinguibilis ramulis rubellis, foliolis nervibus centralibus rubellis et indumento pilis basi aurantiaca et apice albescenti, forma foliolorum praecipue elliptica et numero reducto.

Bejucos, trepadores de otros árboles; ramitas fértiles rojizas a cafés o café-grisáceas, esparcidamente hirsuto pelosas, pelos rojizos. Hojas con estípulas deciduas, no vistas; yemas vegetativas axilares 0.5 × 0.2 mm, ovadas. Hojas 7.5–12 cm de largo; pulvino hirsuto; pecíolo 1.2–1.7 cm de largo; raquis 1.8–4 cm de largo, terete, recto; peciólulos 1.2–1.7 mm de largo, hirsutos. Folíolos 5–7, alternos; folíolos laterales 2.2–5.6 × 1.1–2.2 cm, ovados a mayormente elípticos, simétricos, la base obtusa a aguda, el ápice acuminado con un acumen 0.5–1 × 0.4 cm, mucronado, el borde entero, sin pelos, el folíolo terminal 5–6 × 1.5–2 cm, elíptico, base aguda o cuneada, ápice acuminado, todos los folíolos glabros por el envés, excepto por la nervadura media, la cual es hirsuta y estrigosa por el envés, la pubescencia del envés con pelos blanquecinos, pero con la base de color anaranjado a rojizo, dando la apariencia de ser engrosado en la base, la nervadura central prominente por el envés, rojiza; nervación broquidódroma, con nervaduras poco conspicuas entre las nervaduras secundarias; nervaduras terciarias reticuladas poco notorias por el haz y envés. Inflorescencias terminales o agrupándose hacia las axilas distales de las ramitas floríferas, paniculadas, 1.5–3 cm de largo, muy cortamente pedunculadas el pedúnculo 0.5 mm de largo, el pedúnculo y el raquis hirsuto pubescente, pelos café-rojizos, brácteas de las inflorescencias 0.5 × 0.4 mm, triangulares, pajizas, escariosas, flores 5–6 mm de largo, con pubescencia café-rojiza, adpresas al cáliz, el pedicelo de menos de 1 mm, las bractéolas 1 × 0.8 mm, cocleadas, laciniadas en los bordes, estrigulosas, casi glabras, cáliz 2.8 × 2 mm, campanulado, estrigoso, lobos adaxiales de 0.4 × 1 mm, deltoides, los laterales 0.4 × 0.8 mm, deltoides y el abaxial de 0.3 × 0.7 mm, triangular. Estandarte 5 ×4 mm (incluyendo la uña 1.2 mm de largo), lámina suborbicular, alas 4.5–5 × 1.3 mm, quillas 4.5 × 1.3 mm (incluyendo el pie de 1.5 mm de largo), lámina 3 × 1.3 mm, oblonga, auriculada hacia el lado adaxial. Estambres 10, todos unidos formando un collar que abraza al pistilo, este collar abierto por el lado adaxial, estambres 3.8–4.5 mm de largo, la parte unida 3 mm de largo, anteras 0.3 × 0.2 mm, ovadas. Disco nectarífero oblicuo, completamente abierto por el lado abaxial con el extremo más largo hacia el lado adaxial (de 0.6 mm de largo en su punto más largo). Pistilo de 4.4 × 0.7 mm, pie 1 mm de largo, glabrescente, estilo 1 mm de largo, glabro. Frutos no vistos. Semillas maduras no vistas.

Distribución, hábitat y fenología.—Conocida de una sola colección en la región de Golfo Dulce, en el sur de Costa Rica, probablemente en bosques lluviosos. Florece en julio-agosto y fructifica probablemente en enero–marzo.

Etimologia.—El nombre se refiere a las nervaduras marcadamente rojizas y contrastantes con la lámina foliar.

Discusión.—Esta especie es muy distintiva por sus ramitas rojizas, hojas con nervaduras centrales rojizas

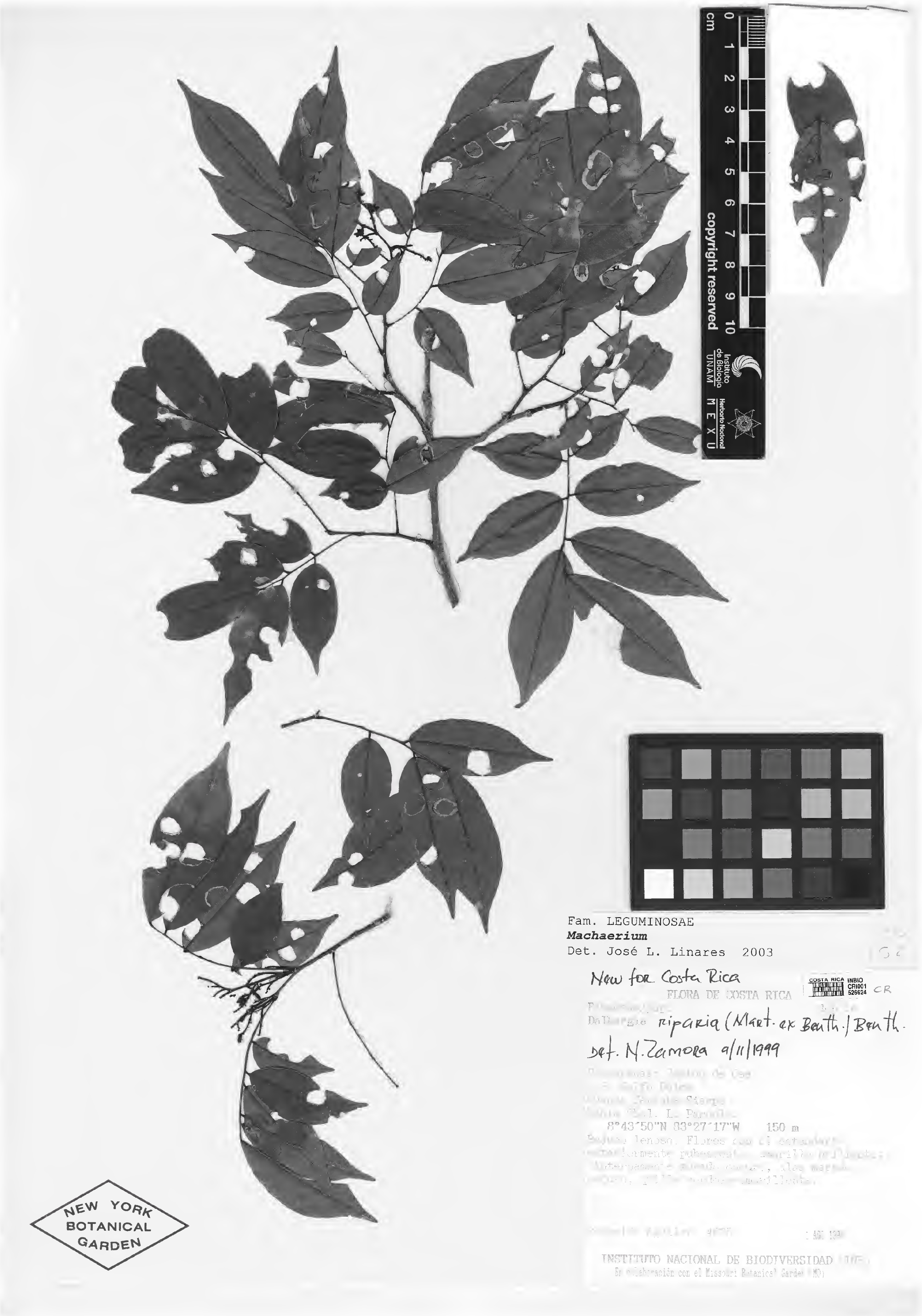
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FIG. 4. *Machaerium rubrinervium* J. Linares. Imagen escaneada del espécimen tipo (*R. Aguilar 4635*, NY).

y por el indumento formado por pelos con la base anaranjada y el ápice blanquecino. Además, la forma de los folíolos, mayormente elípticos y en número reducido es también muy característica.

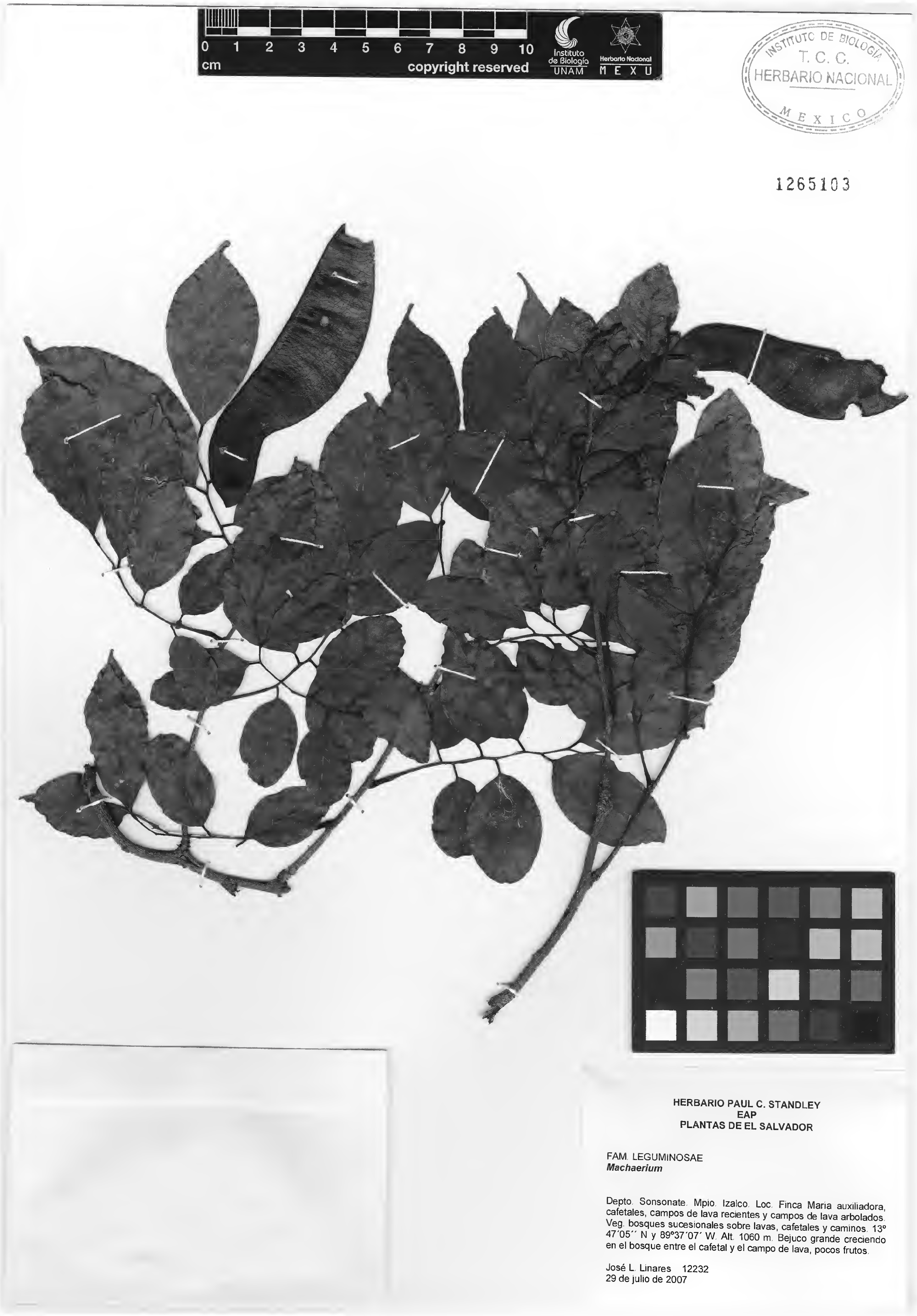
Machaerium franksullyvanii J. Linares, sp. nov. (**Figs. 5, 6**). Tipo: EL SALVADOR. Sonsonate: Mpio. Izalco, Finca María Auxiliadora, campos de lava recientes y campos de lava arbolados, 13°47'05"N y 89°37'07"O, 1060 m, 29 jul 2007, *J.L. Linares 12232* (holotipo: MEXU).

Species *M. pittieri* Macbride similis sed foliis margine repando (forte undulato) petalis carinae conduplicatis latere abaxiali, fructibusque glandibus circularibus depressis, margine adaxiali insigniter incrassato, usque ad 2 mm crassum, habitatione campis lavae et silvis montanis inter 1000 et 2000 m differt.

Bejucos muy grandes, de hasta 10–15 m de largo, trepadores de otros árboles, a veces reportado como arbolito de 3–5 m, dentro del sotobosque, pero mayormente bejuco; ramitas floríferas pardas, grisáceas o café, conspicuamente lenticeladas, glabras; hojas con estípulas de 5–8 × 2–3 mm, glabras, triangulares, cocleadas, algo falcadas, papiráceas o pajizas, persistentes; yemas vegetativas axilares, presentes sólo en ramas estériles jóvenes, inconspicuas, con dos brácteas diminutas, de 1 mm o menos; hojas 10–21.5(–24) cm de largo, pulvino glabro o glabrescente, pecíolo (1.5–)2.3–3 cm de largo, glabro, comúnmente el peciolo subtendido por una bráctea cimbiforme de 3 mm de largo y ancho, con pelos adpresos blanquecinos; raquis 4–8 cm de largo, terete, algo flexuoso, glabro o glabrescente; peciolulos 5–7 mm de largo, glabros o glabrescentes; folíolos 7(–9), alternos, folíolos laterales 2.6–7 × 1.4–4 cm, ovados a elípticos, base aguda a obtusa, la base aguda a obtusa, el margen repando u ondeando y ápice de hasta 8 mm de largo, retuso y, en material de herbario comúnmente doblado, folíolo terminal de 5–9 × 2.5–4 cm, ampliamente elíptico, obovados u oblongo, la base atenuada a cuneada, el margen repando u ondeado y el ápice acuminado, con un acumen de hasta 9 mm de largo, similar al de los foliolos laterales, todos los folíolos completamente glabros en el haz y en el envés, excepto por unos cuantos pelos estrigosos en los pulvinos jóvenes, las nervaduras primaria, secundarias y hasta de tercer orden, aplanadas en el haz y prominente por el envés; nervación broquidódroma, con nervaduras conspicuas entre las nervaduras secundarias; nervaduras terciarias reticuladas y muy notorias por el envés. Inflorescencias mayormente terminales, si axilares restringidas a las últimas 2–3 hojas de las ramas, generalmente simples o en fascículos de 2–3 inflorescencias, a veces paniculadas, especialmente las terminales, naciendo en ramitas del año, 1.5–7 cm de largo, pedúnculo de 0.5–1 mm de largo, generalmente con una bráctea 4 × 1.5 mm, cimbiforme emarginada, brácteas de la inflorescencia 1 × 0.5 mm, cuculadas, papiráceas, seríceas, el pedúnculo y el raquis estrigoso a seríceo, la pubescencia de tricomas ferrugíneos a café-dorado; Flores 8–9 mm de largo, pediceladas, el pedicelo 0.2–0.6 mm de largo, las bractéolas 1.5 × 2.5 mm, reniforme cuando aplanadas, traslapadas y formando un involucro redondeado, subadpresas a patentes, cáliz 2.3–4.5 × 4 mm, campanulado, estrigoso a seríceo, los lobos del cáliz irregulares, los adaxiales o vexilares 0.5 × 2 mm, en forma de triángulo, los laterales 0.5 × 1.5 mm, triangulares a obtusos y el abaxial 0.5 × 1 mm, redondeado. El estandarte 6–8 × 5–7.5 mm, incluyendo la uña 0.5 × 1–1.5 mm, la lámina reniforme a suborbicular, con el ápice retuso, seríceo hacia la nervadura media por la cara adaxial; alas 7 × 3 mm (incluyendo la uña 1.5 mm de largo, curveada, casi sigmoide), lámina 5.5 × 3 mm, obovada, glabras, quillas 7–7.5 × 2.5–3 mm, (incluyendo la uña de 1.5 mm), la lámina 5.5–6 × 2.5–3 mm, se semiorbicular, auriculada, glabra. Estambres 10, diadelfos (9:1), 6–7.5 mm, la parte unida de 3.5 mm el vexilar de 5 mm, anteras 0.6 mm × 0.5 mm, ovadas, el disco nectarífero de 0.5 × 0.6 mm, urceolado a tubular; pistilo 6 × 1.5 mm, pie 1.5 mm de largo, estilo 1.3 mm de largo, cuerpo 2.5–3 × 1.5 mm, oblongo, villoso, el pedicelo y el estilo glabros. Frutos 7–10.5 × 1.5–2.5 cm (incluyendo el pedicelo de 1–1–3 cm), cámara seminífera 2.7–3 × 1.4 cm, el ala 4.7–5 × 1.9–2.2 cm, ambas con nervaduras muy marcadas, frutos oblongos, el margen adaxial recto o casi recto y conspicuamente engrosado, hasta 2 mm de grueso, el abaxial ligeramente sigmoide, obtuso, surcado en la cámara seminífera. Semillas maduras 19–20 × 10–11 × 4–5 mm, reniformes, algo rugosas, hilo de 1 mm, linear.

Distribución, hábitat y fenología.—Conocida hasta ahora sólo de la región suroccidental de El Salvador, en la sierra de Apaneca-Lamatepec, de 1000–1900(–2000) msnm en selvas medianas subcaducifolias, bosques de niebla, vegetación derivada y cafetales, bordes de caminos.

Etimologia.—Es un placer dedicar esta especie al MSc. Frank Sullyvan Cardoza (1976–), joven apasiona-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PLANTAS DE EL SALVADOR

FAM. LEGUMINOSAE
Machaerium

Depto. Sonsonate. Mpio. Izalco. Loc. Finca Maria auxiliadora, cafetales, campos de lava recientes y campos de lava arbolados. Veg. bosques sucesionales sobre lavas, cafetales y caminos. 13° 47´05´´ N y 89°37´07´ W. Alt. 1060 m. Bejuco grande creciendo en el bosque entre el cafetal y el campo de lava, pocos frutos.

José L. Linares 12232
29 de julio de 2007

Fig. 5. Espécimen tipo de *Machaerium franksullyvanii* J. Linares (*J.L. Linares 12232*, MEXU!).

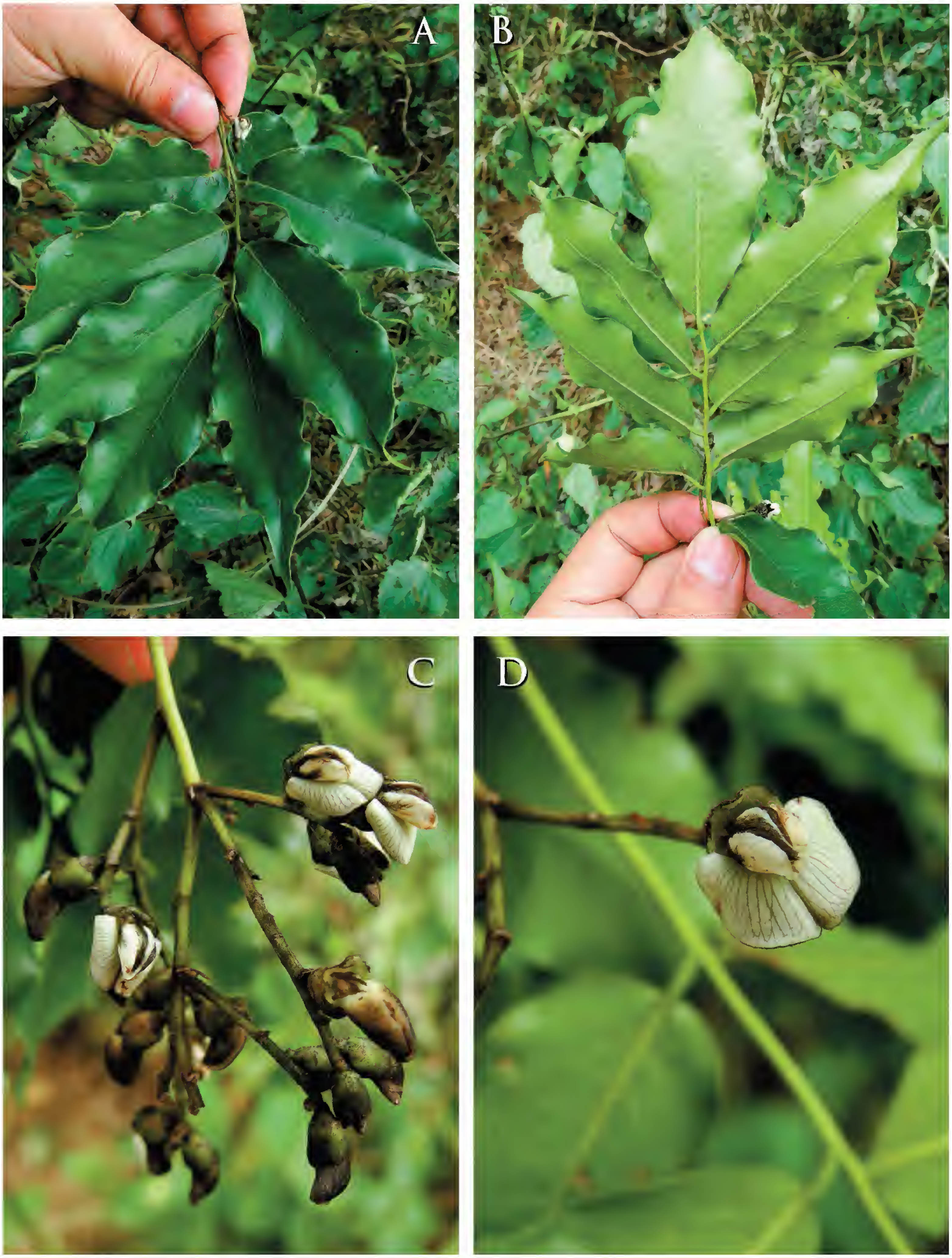

Fig. 6. *Machaerium franksullyvanii* J. Linares. Hoja mostrando el haz (**a**), envés (**b**), nótese los bordes de los foliolos claramente repandos; detalle de la inflorescencia (**c**), flor ampliada (**d**).

do de la botánica, que durante años ha participado en la colecta, identificación y fotografía de la diversidad vegetal en Mesoamérica. Su contribución ha ayudado a documentar la biodiversidad alojada en esta región. Frank ha participado como voluntario poniendo su destreza como fotógrafo y su patrocinio al servicio de algunas expediciones botánicas. Estamos seguros que seguiremos contando con él en nuevas expediciones florísticas.

Florece en marzo y abril y fructifica de enero a marzo del siguiente año.

Nombre vernacular.—Bejuco de uña de gato, bejuco de flores negras.

Material examinado.—**EL SALVADOR. Ahuachapan:** Mpio. San Francisco Menéndez, El Imposible, San Benito, en Cerro Campana, 13°49'N y 89°56'O, bejuco de ca. 23 m, flores negras, abr 1992, *Sandoval y Chinchilla 375* (MEXU); Mpio. Apaneca, 5 km antes de Apaneca, 13°52'N y 89°45'O 1100 m, arbusto escandente con tallos leñosos, creciendo a orilla de calle, hojas compuestas imparipinnadas, frutos de color verde claro, sep 1997, *R. Villacorta y M. Renderos* (*RV-02589*) (MEXU); Mpio. Ataco, Las Oscuranas, oct 2006, *J. Linares, J.F. Gutiérrez y J.E. Castillo s.n.* (MEXU). **Sonsonate:** Mpio. Izalco, Campos de lava del volcán de Izalco, ca. 1 km al S de la Finca La Macarena, al N del cantón Cruz Grande, 13°59'N y 89°39'O, 1100–1200 msnm, arbusto achaparrado de copa densa, sin espinas, feb 2000, *J. Linares 4889* (MEXU); Mpio. Izalco, Campos de lava reciente y campos de lava arbolados, Veg. Bosques sucesionales sobre lavas, cafetales y caminos, 13°47'05"N y 89°37'07"O, 1060 msnm, bejuco grande creciendo en el bosque entre el cafetal y campo de lava, pocos frutos, jul 2007, *J. Linares 12232* (MEXU); idem, arbol débil de 4 m, creciendo en el cafetal, muchos frutos, jul 2007, *J. Linares 12239* (MEXU); idem, bejuco, frutos verdes, ago 2007, *J. Linares 12293* (MEXU).

Discusión.—Esta distintiva especie resalta por su hábito vegetativo como bejuco o arbusto aparrado de gran tamaño con numerosas ramas escandentes cubriendo una extensión relativamente grande, a veces trepando sobre árboles cuando crece en bosques o creciendo como parras aisladas en campos de lava vieja; sus folíolos presentan márgenes o bordes repandos, es decir, muy ondeados, con aspecto de haber sido secados en forma defectuosa, pero es una característica claramente visible en vivo. Por otro lado, en cuanto a las flores, destaca el cáliz con los dientes o lobos inconspicuos, el estandarte casi orbicular, la quilla con uno o sus dos pétalos claramente conduplicados en el margen abaxial. Además, sus frutos presentan, al menos cuando jóvenes, pubescencia estrigosa en todo el cuerpo, glándulas circulares depresas más oscuras, a veces inconspicuas, y una sutura vexilar muy engrosada de hasta 2 mm.

AGRADECIMIENTOS

A las autoridades de la UNAH y CURLA, especialmente a Jean O. Rivera y Eydi Yanina Guerrero que apoyaron la finalización de este trabajo, a Fernando Chiang Cabrera que facilitó mis estancias en la Ciudad de México durante la realización de este trabajo, a Cyrill Nelson Hardy Sutherland (Cyril Hardy Nelson Sutherland) por sus diagnosis en latín y sus valiosas sugerencias al manuscrito, a Gloria y Mario Sousa por su inestimable ayuda en el herbario Nacional de México (MEXU), a María del Rosario García Peña (Maru) por su ayuda en el manejo de los préstamos dentro y fuera de México, a dos revisores anónimos que contribuyeron a mejorar notablemente el manuscrito, a Frank Sullyvan Cardoza Ruíz y Ana Eugenia Aguilar por su ayuda en los viajes de campos en El Salvador y Honduras, a los curadores de los Herbarios CAS, DS, F, LL, MEXU, MO, NY y US por poner a mi disposición gran cantidad de material para su estudio.

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BOOK REVIEW

Susan Leopold, with illustrations by Nicky Staunton. 2014. **Isabella's Peppermint Flowers.** (ISBN 978-0-692-33302-0) (**Orders:** www.FloraForKids.org). $18.00 US, 36 pp., watercolor drawings, glossary, epilogue.

For the young aspiring botanist, this book will be a treasure. The story of two girls who go flower-hunting with their mother becomes an introduction to the basics of botany, augmented by the excellent illustrations. The author incorporates the historical context of botanical pioneers including an introduction to Linneaus, John Clayton, and John Gronovius in the State of Virginia. Terms and names used in the context of the story are clarified in the definitions at the end. This book is an excellent teaching text for beginning botanists.—*Pamela Edmondson, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas, U.S.A.*

What a fantastic and unique resource for both children and their caretakers! Author Susan Leopold uses the story of two sisters and a mother walking in the woods to introduce the basics of taxonomy, floristics, and plant collecting, all while dropping in asides about binomial nomenclature, rare and endangered species, and botanical history. True, the story focuses in part on the history of the flora of Virginia, but the overall message is universal: inspiring a sense of place and an appreciation of the natural world. For the sake of encouraging a new generation of botanists, it would be a wonderful thing to see books like this for all 50 states.—*Brooke Byerley Best, PhD, Editor & Botanist, Botanical Research Institute of Texas, Fort Worth, Texas, U.S.A.*

BOOK NOTICE

Larry J. Littlefield & Pearl M. Burns. 2015. **Wildflowers of the Northern and Central Mountains of New Mexico: Sangre de Cristo, Jemez, Sandia, and Manzano.** (ISBN-13: 978-0-82635-547-8, pbk.). University of New Mexico Press, 1717 Roma Avenue NE, Albuquerque, New Mexico 87106, U.S.A. (**Orders:** www.unmpress.com, 1-800-249-7737). $29.95 US, 408 pp., 419 color plates, 1 map, 5.5" × 8.5".

From the publisher: This unique reference work describes over 350 wildflowers and flowering shrubs that grow in New Mexico's Sangre de Cristo, Jemez, Sandia, and Manzano mountains, as well as neighboring ranges, including the Manzanita, San Pedro, Ortiz, and other lower-elevation mountains in central portions of the state. With more than a thousand color photographs accompanied by visual descriptions, the easy-to-use guide organizes plants first by flower color, then alphabetically by family common name, then by scientific name. The authors also include information on traditional uses of the plants by indigenous peoples and an extensive glossary and bibliography. A brief geological history and description of the ranges examines the different life zones and ecosystems and how these relate to elevation and microclimates. Wildflower enthusiasts and hikers will welcome this useful book.

Larry J. Littlefield is a professor emeritus of plant pathology at Oklahoma State University. He has been a volunteer with the Sandia Mountain Natural History Center and the trails maintenance crew for the U.S. Forest Service since retiring in Albuquerque in 2005.

Pearl M. Burns, coauthor of the "Wildflowers" chapter of *Field Guide to the Sandia Mountains* (UNM Press), is a member of the Friends of the Sandia Mountains and a leader of countless wildflower hikes for the U.S. Forest Service, Albuquerque Open Space program, and other organizations.

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GNAPHALIOTHAMNUS NESOMII (ASTERACEAE: GNAPHALIEAE), A NEW SPECIES FROM GUATEMALA AND NOMENCLATORIAL CHANGES

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ABSTRACT

Gnaphaliothamnus nesomii M.O. Dillon & Luebert (Asteraceae: Gnaphalieae) is a new species from the Sierra de los Cuchumatanes, Department Huehuetenango, Guatemala. The generic boundaries within the Gnaphalieae have been controversial and the genus *Gnaphaliothamnus* has not been universally accepted. New molecular phylogenetic studies support the acceptance of *Gnaphaliothamnus* as distinct from *Chionolaena*, which is congruent with cypsela trichome morphology. Two *Gnaphalium* species are transferred as **Pseudognaphalium stolonatum** (S.F. Blake) M.O. Dillon and **P. paramorum** (S.F. Blake) M.O. Dillon.

Key Words: *Chionolaena*, *Gamochaeta*, *Gnaphaliothamnus*, *Gnaphalium*, *Pseudognaphalium*, Asteraceae, Gnaphalieae, Gnaphaliinae, Guatemala, *Lucilia*-group, comb. nov., sp. nov., Sierra de los Cuchumatanes, taxonomy

RESUMEN

Gnaphaliothamnus nesomii M.O. Dillon & Luebert (Asteraceae: Gnaphalieae), es una nueva especie proveniente de Sierra de los Cuchumatanes, Departamento Huehuetenango, Guatemala. Los límites genéricos en Gnaphalieae son controvertidos y el género *Gnaphaliothamnus* no ha sido universalmente aceptado. Nuevos estudios filogenéticos moleculares apoyan la aceptación de *Gnaphaliothamnus* como un género diferente de *Chionolaena*, lo que es congruente con la morfología de los tricomas de las cipselas. Dos especies de *Gnaphalium* son transferidas como **Pseudognaphalium stolonatum** (S.F. Blake) M.O. Dillon y **P. paramorum** (S.F. Blake) M.O. Dillon.

Palabras Clave: *Chionolaena*, *Gamochaeta*, *Gnaphaliothamnus*, *Gnaphalium*, *Pseudognaphalium*, Asteraceae, Gnaphalieae, Gnaphaliinae, Guatemala, *Lucilia*-group, comb. nov., sp. nov., Sierra de los Cuchumatanes, taxonomy

INTRODUCTION

Gnaphaliothamnus Kirp. (Asteraceae, Gnaphalieae) comprises around 11 species distributed from Mexico to Costa Rica. It has been accepted (Nesom 1990a,b; 1994) or subsumed in the South American *Chionolaena* DC. (Anderberg & Freire 1989, 1991; Freire 1993; Nesom 2001; Freire et al. 2015). Based upon differences in cypselar (achenial) trichomes, Dillon (2003) argued that *Gnaphaliothamnus* was a monophyletic group not necessarily close to *Chionolaena*. The cypselar trichomes in *Gnaphaliothamnus* are described (Hess 1938) as short clavate (*zwillingshaares*) with an enlarged adaxial basal cell (*schwellpolster*) and myxogenic apical cells 65–125 µm long. The two apical cells in the cypselar trichomes in *Chionolaena* are much longer (250–850 µm long) and not myxogenic (Dillon & Sagástegui 1991; Loeuille et al. 2011).

Pruski (2012) transferred a Guatemalan species, *Gnaphalium stolonatum* S.F.Blake, to *Chionolaena*, with the comment that it resembled other Mexican and Central American members. He apparently did not examine the type material of *G. stolonatum*, providing a new description drawn from a herbarium collection that he termed a "topotype" (*A. Molina et al. 16441*, NY). From this voucher, he described the plants as reduced subshrubs to 30 cm tall with clusters of capitula each having 30–70+ pistillate florets and 11–25 hermaphroditic disc florets. He described the cypselas as setose with elongate trichomes, a condition very different from that described for the type by Blake, i.e., minutely hispidulous with conical, bluntish, few-celled, dark-based hairs (Blake 1937). An examination of the holotype of *Gnaphalium stolonatum* (*A.F. Skutch 1098*, GH) has shown it to be distinct from other collections from the same general region annotated as *G. stolonatum*. *Gnaphalium stolonatum* is here treated as a *Pseudognaphalium* Kirp. and transferred to that genus. The other morphologically different collections (e.g., *A. Molina et al. 16441*) are described here as a new species of *Gnaphaliothamnus* from the Sierra de los Cuchumatanes.

In the ultimate offering from H. Robinson (2015), he relegates *Pseudoligandra* M.O. Dillon & Sagást. (1990) and *Gnaphaliothamnus* to the synonymy of *Chionolaena*. He states that the publications by Freire (1993) and Nesom (2001) have "totally resolved that problem by reducing all three genera to synonymy under the name *Chionolaena*." While we have been unsuccessful in extracting DNA from the samples representing *Pseudoligandra* at our disposal, we are confident that our nrDNA results have more definitively resolved the problem of the recognition of *Gnaphaliothamnus* as distinct from *Chionolaena*.

TAXONOMY

Gnaphaliothamnus nesomii M.O. Dillon & Luebert, sp. nov. (**Fig. 1**). Type. GUATEMALA. Huehuetenango: common on moist bank along road to San Juan Ixcoy, Sierra Cuchumatanes, 12–23 Jan 1966, *A. Molina R., W.C. Burger, and B. Wallenta 16441* (holotype: F1637117; isotype: NY, n.v.)

Similar to *Gnaphaliothamnus salicifolius* (Bertol.) G.L. Nesom but habit considerably smaller (to 15 cm tall), capitulescences glomerulate, obscured in dense arachnoid-tomentose indumentum, cypselar trichomes ca. 100 µm long

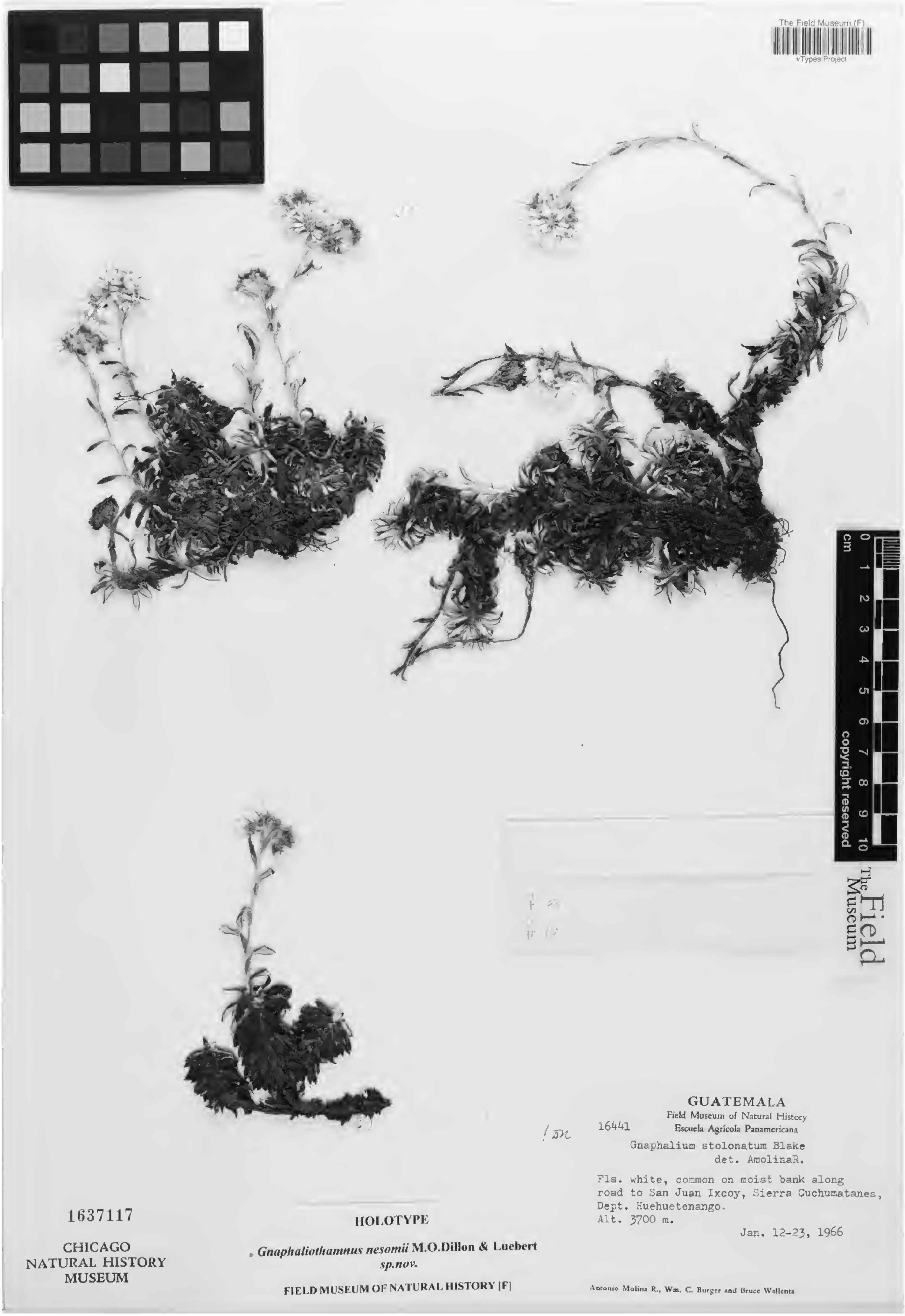
Subshrubs, 5–10(–15) cm tall; stems ascending, basally-branched from lignified base. **Leaves** sessile, oblanceolate to spatulate, 10–42 mm long, 2–4 mm wide, abaxial surfaces white-tomentose, adaxial surfaces darker, weakly arachnoid-tomentose, apices acute, apiculate, proximal leaves marcescent. **Capitulescences** densely glomerulate with 7–11(–20) tightly grouped capitula, pedicles obscured by dense arachnoid-tomentose indumentum. **Capitula** 5–7 mm long, 2–3 mm diam.; involucres narrowly campanulate, graduated, submerged in dense arachnoid-tomentose indumentum; phyllaries 4–6-seriate, the outer with arachnoid-tomentose bases; the inner with white-opaque, oblong apical lamina, 5–7 mm long, ca. 2 mm wide; outer florets 20–32, pistillate, fertile; central disc florets 13–15, hermaphroditic, ovary sterile. **Cypselas** oblong, ca. 1 mm long, trichomes 4-celled, clavate, ca. 100 µm long, the apical cells myxogenic, not rupturing (Fig. 2A); pappus of ca. 20, setose bristles, 2.8–3.2 mm long, apical cells of bristles of hermaphroditic florets expanded, apical cells of pistillate florets obtuse, not expanded.

Etymology.—*Gnaphaliothamnus nesomii* is dedicated to Dr. Guy L. Nesom, noted synanthrologist and systematist, one of the first botanists to accept *Gnaphaliothamnus* in modern usage, and first to provide a detailed revision for Mexican and Central American taxa. Over the years, Dr. Nesom has been generous with his detailed knowledge of Mexican and Central American Asteraceae and particularly the Gnaphalieae. He also commented on the uniqueness of some of the sheets examined within his loan of material from Field Museum in 1990.

Distribution and Ecology.—The type locality is within the Sierra de los Cuchumatanes in the Department of Huehuetenango, Guatemala [15°31'S, 91°32'W]. This is the highest non-volcanic mountain range in Central America and has the most extensive highlands above 3000 m. The region is home to a variety of different biomes, including montane pine-oak forest, intermittent shrublands, and grasslands. *Gnaphaliothamnus nesomii* is found in alpine habitats at ca. 3700 m, notably different from the environments associated with the "llanos" or plains where *Gnaphalium stolonatum* occurs (see below).

Conservation status.—*Gnaphaliothamnus nesomii* deserves a preliminary status of Critically Endangered (CR) because total area of its known distribution is less than 100 km^2 and only three populations are known (IUCN 2001).

Discussion.—Recent molecular phylogenetic studies (nrDNA) have provided results that suggest the great majority of New World genera of Gnaphalieae are associated with the *Lucilia*-group within the FLAG clade (Freire et al. 2015; Luebert et al., unpubl.). The *Lucilia*-group has been expanded to include *Gnaphaliothamnus*, *Chionolaena*, and *Antennaria* Gaertn. from the subtribe Cassiniinae Anderb. (Anderberg 1991). These results support the hypothesis that the gross morphological similarity between *Gnaphaliothamnus* and *Chionolaena* is convergence; they are found in distant well-supported clades within the *Lucilia*-group (Fig. 3). *Gnaphaliothamnus* is phylogenetically related to *Antennaria*, while *Chionolaena* appears to be sister to a group including the type species of *Lucilia* Cass., which is in agreement with their similarity in cypselar trichomes.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Gnaphalium stolonatum Blake
det. AmolinaR.
Fls. white, common on moist bank along road to San Juan Ixcoy, Sierra Cuchumatanes, Dept. Huehuetenango.
Alt. 3700 m.
Jan. 12-23, 1966
Antonio Molina R., Wm. C. Burger and Bruce Wallenta
1637117
CHICAGO NATURAL HISTORY MUSEUM
HOLOTYPE
Gnaphaliothamnus nesomii M.O.Dillon & Luebert sp.nov.
FIELD MUSEUM OF NATURAL HISTORY [F]

Fig. 1. *Gnaphaliothamnus nesomii*. Photograph of holotype collection, *A. Molina R. et al. 16441* (F1637117, imgV0093984F).

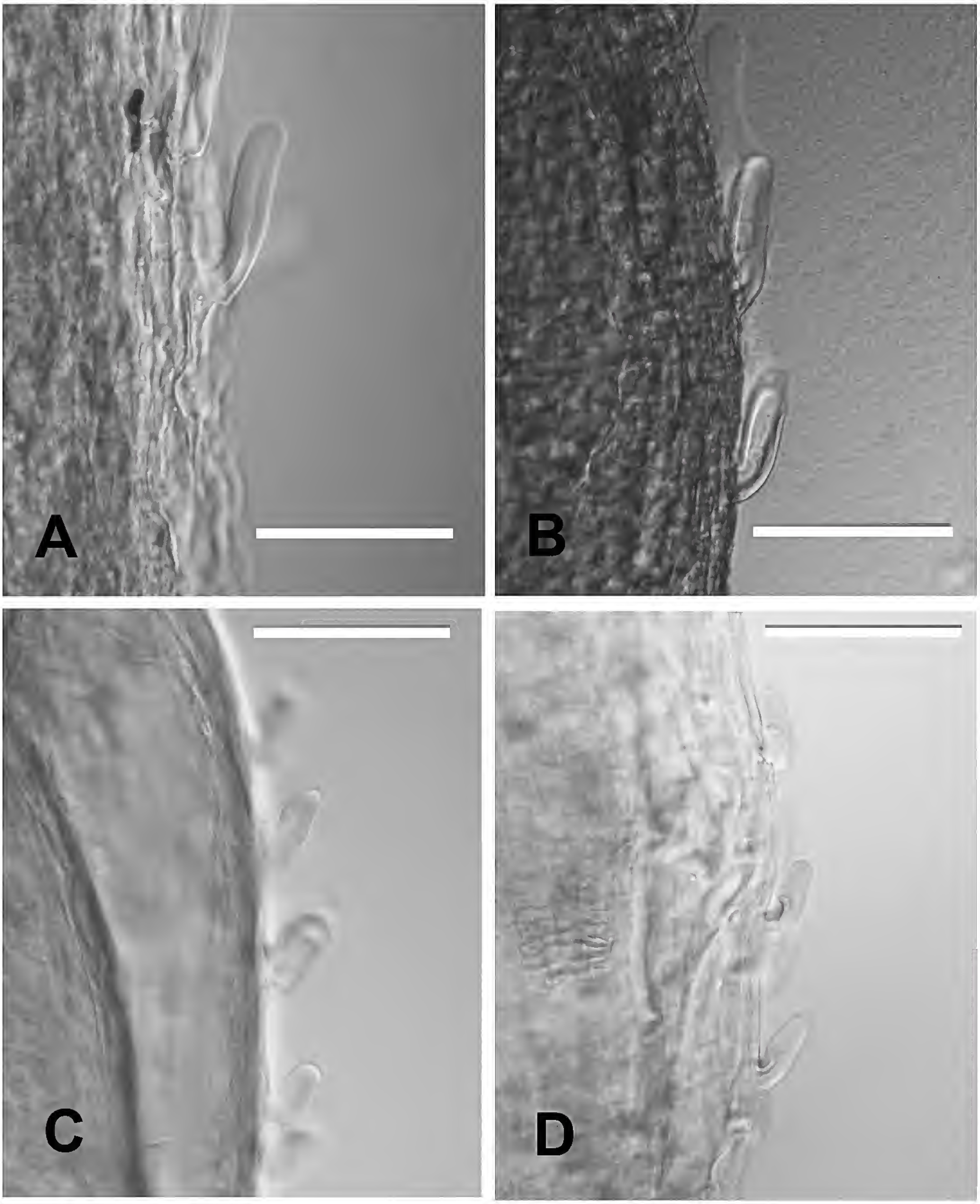


Fig. 2. Cypselar trichomes, white scale bar = 100 µm. **A.** *Gnaphaliothamnus nesomii* (F1637117), **B.** *G. salicifolius* (F1639348), **C.** *Pseudognaphalium stolonatum* (GH00008351), **D.** *P. antennarioides* (F1148157).

Nesom (1990a) provided a detailed taxonomic history for *Gnaphaliothamnus* and his rationales for its acceptance (Nesom 1990b, 1994). Interestingly, Nesom also discussed the putative relationships for *Gnaphalium stolonatum* as outside of *Gnaphaliothamnus* (Nesom 1990a, p. 367). He commented that this taxon did have white-tipped phyllaries, but it had more florets per capitulum in general (+100) and fertile central disc florets,

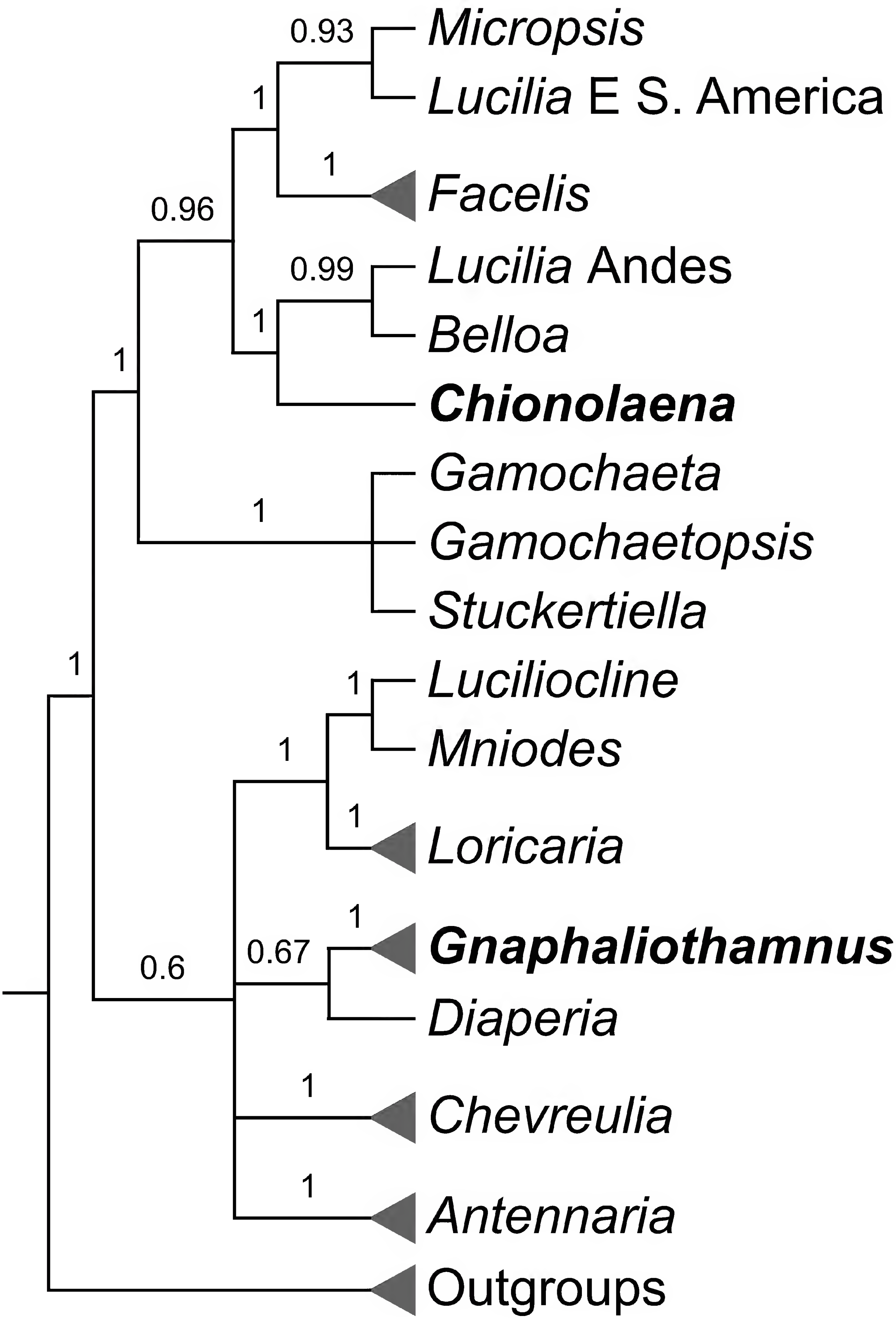

0.93
Micropsis
Lucilia E S. America
1
1
Facelis
0.96
0.99
Lucilia Andes
1
Belloa
1
Chionolaena
Gamochaeta
1
Gamochaetopsis
Stuckertiella
1
1
Luciliocline
1
Mniodes
1
Loricaria
1
0.67
Gnaphaliothamnus
0.6
Diaperia
1
Chevreulia
1
Antennaria
Outgroups

Fig. 3. Simplified cladogram of the *Lucilia*-group derived from preliminary result of a Bayesian analysis of Gnaphalieae with nrDNA sequence data (ITS+ETS) carried out in MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003). The numbers above branches are Bayesian posterior probabilities. The results are congruent with those reported by Freire et al. (2015). *Chionolaena* and *Gnaphaliothamnus* do not form a clade.

Table 1. Comparison of salient morphological characters in the species of *Gnaphaliothamnus* and *Pseudognaphalium* discussed here. Cypselar trichomes are illustrated in Figure 2.

Character	*G. nesomii*	*G. salicifolia*	*P. stolonatum*	*P. antennarioides*
Habit	subshrubs to 15 cm	subshrubs to 100 cm	perennial herbs	perennial herbs
Stolons	none	none	present	present
Capitula height	5–7 mm	6–7	4.5–5.5 mm	6–7 mm
Pistillate florets	20–32	(22–)34–55	44–92	(50–)75–190
Hermaphroditic florets	13–15	3–4(–7)	7–14	7–16
Cypselar trichomes	ca. 100 µm long, Fig. 2A	62–78 µm long, Fig. 2B	38–40 µm long, Fig. 2C	ca. 50 µm long, Fig. 2D

and suggested it was probably best maintained in *Gnaphalium* L. *s.s.* There has been acceptance of *Pseudognaphalium* and the majority of New World species previously classified as *Gnaphalium* were transferred there (Anderberg 1991).

Gnaphaliothamnus nesomii was originally treated as *Gnaphalium stolonatum*. In a note from Guy Nesom (16 Feb 1990) accompanying the return of his Field Museum loan, he mentioned the presence of some unusual or atypical specimens with fewer pistillate florets. When Pruski (2012) encountered what he considered conspecific material (*A. Molina 16441*, NY), he transferred the species to *Chionolaena* and described its floral morphology exactly as it is in *Gnaphaliothamnus*. He related it to other Mexican and Central American species, including *C. eleagnoides* Klatt, C. *lavandulifolia* (Kunth) Benth & Hook. f., *C. concinna* (A. Gray) Anderb. & S. E. Freire (as *C. mexicana* S. E. Freire), and *C. salicifolia* (Bertol.) G.L. Nesom, all species considered here to belong within *Gnaphaliothamnus*.

Gnaphaliothamnus nesomii is distinctive among members of *Gnaphaliothamnus*. It has a dwarf woody vegetative habit with stems only 5–10(–15) cm long, the basal leaves are marcescent and cloaking the lower portions of the stems, and the glomerulate capitulescences with the heads immersed in dense, white, arachnoid-tomentose indumentum, is a combination of characteristics unmatched in the genus. It has oblanceolate to spathulate leaves to 42 mm long, white-opaque phyllary apices, and capitula with 20–32 pistillate florets, and 13–15 hermaphroditic florets, Nesom's (1990a) key would lead to *G. salicifolius*; which is the only other member of *Gnaphaliothamnus* to be recorded from Guatemala, and it has a widespread distribution extending north from Guatemala to central Mexico.

Gnaphaliothamnus salicifolius has a distribution quite unlike all other species, which tend to be narrowly endemic and geographically restricted (Nesom 1990a,b, 1994). In Guatemala, it inhabits the edge of pine-oak forests at about 3000 m and is also found in the Sierra de los Cuchumatanes, recorded on the road between Paquix and San Juan Ixcoy (*A. Molina R. 21293,* F1661761; *A. Molina R. et al. 30031,* F1734420; *A. Molina R. et al. 16550,* F1639348) and N of Santa Eulalia (*F. Almeda and J.L. Luteyn 1686,* F1733978).

Table 1 allows for comparison of the salient morphological characteristics of three of the Gnaphalieae taxa known to occur in region around the Sierra de los Cuchumatanes.

Additional material examined: **GUATEMALA. Huehuetenango:** Sierra Cuchumatanes between Paquix and San Juan Ixcoy, 8 Jan 1974, 3000–3350 m, *A. Molina R., A.R. Molina, and J.A. Molina 30055* (F1734422); between Tojquiá and Caxín bluff, summit of Sierra de los Cuchumatanes, 3700 m, 6 Aug 1942, *J.A. Steyermark 50159* (F1148150).

KEY TO *GNAPHALIOTHAMNUS* SPECIES

The following annotated key will allow for identification of *Gnaphaliothamnus* species (adapted from Nesom 1990a):

1. Inner phyllaries lacking prominent, white lamina; pappus bristles monomorphic (Chiapas - Mexico) __________ **G. cryptocephalus** G.L. Nesom

1. Inner phyllaries with prominent, white lamina.
  2. Adaxial leaf surfaces with stipitate glandular trichomes beneath the arachnoid-tomentum.
    3. Pistillate florets 5–10; pappus bristles strongly dimorphic, caducous; cypselas glabrous (Costa Rica) __________ **G. costaricensis** G.L. Nesom

3. Pistillate florets 12–24; pappus bristles monomorphic to weakly or strongly dimorphic, basally persistent; cypselas with trichomes.
    4. Pistillate florets 12–18, usually equal the number of hermaphroditic; pappus bristles strongly dimorphic (Oaxaca - Mexico) ____ **G. macdonaldii** G.L. Nesom
    4. Pistillate florets 21–24, usually about twice as many as the hermaphroditic; pappus bristles monomorphic to very weakly dimorphic (Veracruz, Puebla, Tlaxcala, Morelos - Mexico) ____ **G. lavandulifolius** (Kunth) G.L. Nesom

2. Adaxial leaf surfaces arachnoid-tomentose to glabrate, eglandular.
    5. Leaves 7–8 mm long; phyllaries subequal (Oaxaca - Mexico) ____ **G. sartorii** (Klatt) G.L. Nesom
    5. Leaves shorter than 5 mm or longer than 10 mm long; phyllaries strongly graduated.
        6. Heads few in tight clusters at tips of leafy stems.
            7. Plants dioecious; leaves 2.5–5 mm long; phyllaries with reddish midregion (Oaxaca - Mexico) ____ **G. aecidiocephalus** (Grierson) G.L. Nesom
            7. Plants polygamodioecious; leaves 10–20 mm long; phyllaries without a red midregion (San Luis Potosí - Mexico) ____ **G. concinnus** (A. Gray) G.L. Nesom
        6. Heads numerous in corymbs above the leaves.
            8. Leaves elliptic to elliptic-oblanceolate; pappus bristles weakly dimorphic.
                9. Leaves elliptic to elliptic-oblanceolate, 15–42 mm long, 4–8 mm wide (Hidalgo, Oaxaca - Mexico) ____ **G. eleagnoides** (Klatt) G.L. Nesom
                9. Leaves elliptic-obovate, 10–20 mm long, 3–5 mm wide (Durango - Mexico) ____ **G. durangensis** G.L. Nesom
            8. Leaves linear to oblanceolate or spathulate; pappus bristles strongly dimorphic.
                10. Leaves 20–80 mm long, 1–3(–5) mm wide; pistillate florets (22–)34–55; hermaphroditic florets 3–4(–7) (Guatemala, Mexico) ____ **G. salicifolius** (Bertol.) G.L. Nesom
                10. Leaves 10–42 mm long, 2–4 mm wide; pistillate florets 20–32; hermaphroditic florets 13–15 (Guatemala) ____ **G. nesomii** M.O. Dillon & Luebert

NEW COMBINATIONS IN *PSEUDOGNAPHALIUM*

Pseudognaphalium stolonatum (S.F. Blake) M.O. Dillon, comb. nov. (**Fig. 4**). *Gnaphalium stolonatum* S.F. Blake, Brittonia 2:341. 1937. Type: GUATEMALA. Huehuetenango: llanos of the Sierra Cuchumatanes, 10,500 ft [3200 m], 24 Aug 1934, *A. F. Skutch 1098* (holotype: GH00008351; isotype: TEX-LL00373732, n.v.).

Chionolaena stolonata (S.F. Blake) Pruski, Phytoneuron 2012-1:4. 2012.

Perennial herbs 10–25 mm tall, roots fibrous; stolons from the base, filiform; stems erect, usually simple, rarely branched, thinly arachnoid-tomentose, purplish. **Leaves** oblanceolate to linear, 2–4.5 mm long, 0.5–1 mm wide, abaxial surfaces gray with dense tomentose indumentum, adaxial surfaces obscurely stipitate-glandular under thinly arachnoid-tomentose indumentum, apices apiculate, bases slightly decurrent. **Capitulescences** glomerulate, crowded at apices. **Capitula** campanulate, sessile, 4.5–5.5 mm tall, 4.5–5.5 mm diam.; phyllaries ca. 4-seriate, graduated, thinly arachnoid-tomentose; outer ovate to oblong-lanceolate, obtuse to acute, inner narrowly lanceolate, narrowed to an obtuse apex; pistillate florets 85–92, the corollas filiform, white, ca. 2.5 mm long, pappus bristles ca. 3 mm long, apices acute; hermaphroditic florets (7–)11(–14), the corollas cylindrical, white with rose-color lobes, the styles apically subtruncate, ovary sterile; pappus bristles ca. 3 mm long, apically obtuse, slightly expanded. **Cypselas** ca. 1 mm long, minutely hispidulous, the trichomes clavate, 38–40 µm long (Fig. 2C).

Pseudognaphalium stolonatum has been collected within the Sierra de los Cuchumatanes from alpine meadows on rock outcrops, 3200–3750 m. It was included in *Gnaphalium s.s.* by Anderberg (1991). Inspection of the type has shown it to have floral morphology consistent with *Pseudognaphalium* (Anderberg 1991).

Blake (1937) specifically related *Pseudognaphalium stolonatum* to *P. antennarioides* (DC.) Anderb., a rosulate, stoloniferous herb distributed from Colombia to Bolivia with capitula having (50–)75–190 pistillate and 7–16 hermaphroditic florets. Phylogenetic studies have shown that *Pseudognaphalium* is a member of the HAP clade (Smissen et al. 2011; Nie et al. 2013; Galbany-Casals et al. 2014), along with *Achyrocline* (Less.) DC., *Helichrysum* Mill., and *Anaphalis* DC.; *Gnaphaliothamnus* and *Chionolaena* are members of the FLAG clade, which is only distantly related (Smissen et al. 2011).

Pseudognaphalium subsericeum (S.F. Blake) Anderb. (= *Gnaphalium subsericeum* S.F. Blake, 1927), a Costa Rican endemic, was also mentioned as potentially related to *Gnaphaliothamnus salicifolius* by Blake (p. 62). An examination of conspecific material from Costa Rica (F1692005, F1692006) shows *P. subsericeum* more simi-

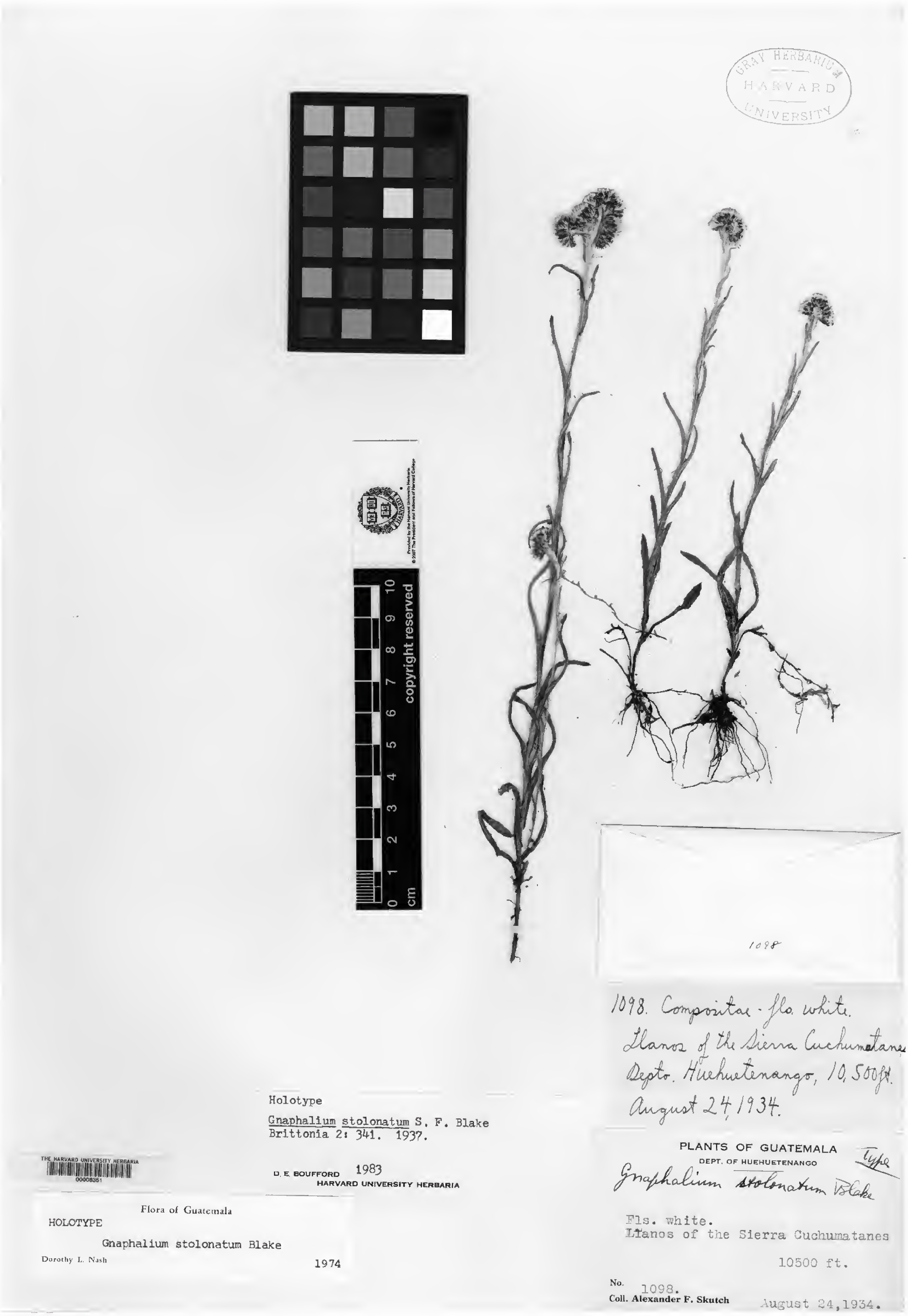
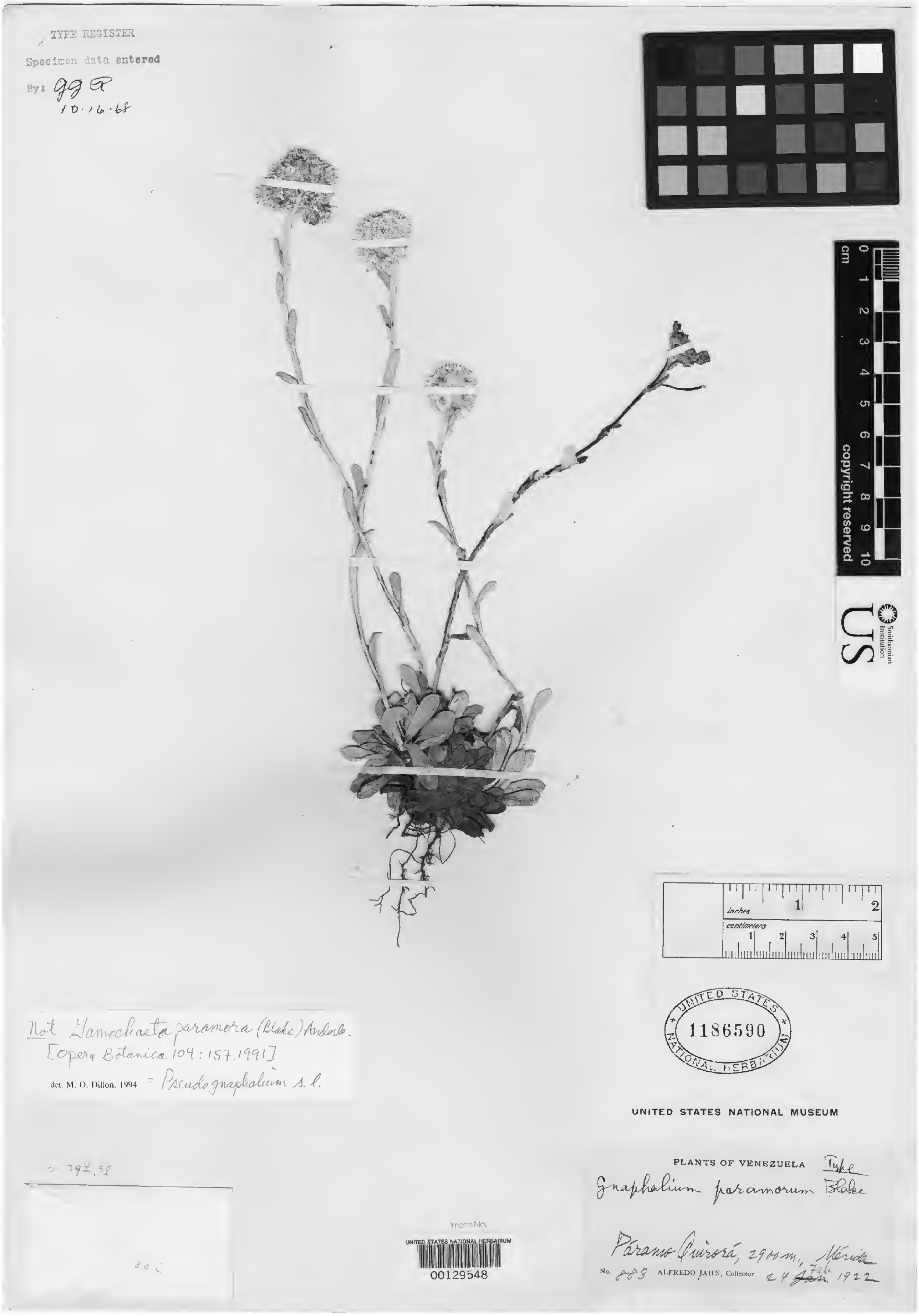

GRAY HERBARIUM
HARVARD
UNIVERSITY
copyright reserved
cm
0 1 2 3 4 5 6 7 8 9 10
1098
1098. Compositae - flo. white.
Llanos of the Sierra Cuchumatanes
Depto. Huehuetenango, 10,500 ft.
August 24, 1934.
PLANTS OF GUATEMALA
DEPT. OF HUEHUETENANGO
Type
Gnaphalium stolonatum Blake
Fls. white.
Llanos of the Sierra Cuchumatanes
10500 ft.
No. 1098.
Coll. Alexander F. Skutch
August 24,1934.
Holotype
Gnaphalium stolonatum S. F. Blake
Brittonia 2: 341. 1937.
D. E. BOUFFORD 1983
HARVARD UNIVERSITY HERBARIA
THE HARVARD UNIVERSITY HERBARIA
00008351
Flora of Guatemala
HOLOTYPE
Gnaphalium stolonatum Blake
Dorothy L. Nash
1974

Fig. 4. *Pseudognaphalium stolonatum*. Photograph of holotype collection of *Gnaphalium stolonatum* S.F.Blake, *A.F. Skutch 1098* (GH000008351).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1186590
Not Gamochaeta paramora (Blake) Anderb.
[Opera Botanica 104: 157. 1991]
det. M. O. Dillon, 1994 = Pseudognaphalium s. l.
UNITED STATES NATIONAL MUSEUM
PLANTS OF VENEZUELA Type
Gnaphalium paramorum Blake
Páramo Quirorá, 2900 m, Mérida
No. 883 ALFREDO JAHN, Collector 24 ~~Jan.~~ Feb. 1922
UNITED STATES NATIONAL HERBARIUM
00129548

Fig. 5. *Pseudognaphalium paramorum*. Photograph of holotype collection of *Gnaphalium paramorum* S.F.Blake, *A. Jahn 883* (US1186590, img00129548).

lar to *P. stolonatum* or *P. antennarioides* (DC.) Anderb., the latter an Andean species that has similar overall morphology and cypselar trichomes (Fig. 2D). All these species have capitula in dense cymes or glomerules and phyllaries with showy, white apices.

Additional specimens examined: **GUATEMALA. Huehuetenango:** vicinity of Chemal, summit of Sierra de los Cuchumatanes, 3700–3750 m, 8 Aug 1942, *J. A. Steyermark 50253* (F1148157), *50273* (F1148180), *50275* (F1148179).

Pseudognaphalium paramorum (S.F. Blake) M.O. Dillon, comb. nov. (**Fig. 5**). Basionym: *Gnaphalium paramorum* S.F. Blake, J. Wash. Acad. Sci. 21:328. 1931. Type: VENEZUELA. Estado Mérida: Páramo Quirorá, 2900 m, 24 Feb 1922, *A. Jahn 883* (holotype: US1186590).

Gamochaeta paramora (S.F. Blake) Anderb., Opera Bot. 104:157. 1991.

Blake (1931) commented that *Pseudognaphalium paramorum* had the appearance of *Gnaphalium antennarioides* DC. (= *P. antennarioides* (DC.) Anderb.), and he related it to that taxon, which is a rosulate, stoloniferous herb distributed from Colombia to Bolivia.

Anderberg (1991) transferred *Gnaphalium paramorum* to *Gamochaeta* Wedd.; an examination of the type collection shows it to only superficially resemble *Gamochaeta*. It has a basal rosette of subspathulate leaves and unbranched, ascending stems. The terminal capitulescences are not spicate; they are densely glomerulate corymbs. The type collection has capitular and floral morphology consistent with *Pseudognaphalium*; the cypselas are papillose and lack the 2-celled, sessile trichomes diagnostic for *Gamochaeta*.

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We thank the curators and staff of the herbaria at F, GH, MO, NY, TEX, and US for permitting access to their material. Especially, we wish to acknowledge Ms. Emily Wood, Collections Manager at the Gray Herbarium, who expedited loan of type material from that institution. We thank John Strother for many constructive suggestions in the review process. Andrés Moreira-Muñoz and Miguel Álvarez provided plant material for phylogenetic studies. Digital images were obtained via the Internet in Figure 4 from GH and Figure 5 from US. We thank Field Museum's Christine Niezgoda, Anna Balla, Daniel Le, and Allie Stone for handling various aspects of loans and digitizing collections.

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BOOK NOTICE

Thor Hanson. 2015. **The Triumph of Seeds: How Grains, Nuts, Kernels, Pulses, & Pips Conquered the Plant Kingdom and Shaped Human History.** (ISBN-13: 978-0-465-05599-9, hbk). Basic Books, 250 West 57th St, New York, NY 10107, U.S.A. (**Orders:** www.basicbooks.com, 1-800-343-4499). $26.99 US, 304 pp., 5.75" × 8.5".

From the publisher: Seeds come in all sorts of shapes and sizes—from the miniscule seeds of the spotted coral root to the giant seed of the coco de mar palm tree (also known as a double coconut), which can grow to weigh more than 65 pounds. They are ubiquitous, from tropical rain forests to alpine meadows and the arctic tundra. But more than that, award-winning conservation biologist Thor Hanson writes in his new book [. . .] seeds are vital to life everywhere. "They transcend that imaginary boundary we erect between the natural world and the human world, appearing so regularly in our daily lives, in so many forms, that we hardly recognize how utterly dependent we are upon them," Hanson writes. "Telling their story reminds us of our fundamental connections to nature—to plants, animals, soil, seasons, and the process of evolution itself."

Blending expert, yet understandable explanations of science with humorous first-person reportage and fascinating historical anecdotes, Hanson deftly traces the history and science of seeds, explaining how they nourish, unite, endure, defend, and travel. Seeds, he shows, are quite literally the stuff and staff of life, supporting diets, economies, and civilizations around the globe.

Thor Hanson is a conservation biologist, Guggenheim Fellow, Switzer Environmental Fellow, and winner of the John Burrough Medal for excellence in nature writing and natural history. The author of *Feathers* and *The Impenetrable Forest*, Hanson lives with his wife and son on an island in Washington State.

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NEW COMBINATIONS IN *EUMACHIA* (RUBIACEAE) FOR SPECIES OCCURRING ON THE GUIANA SHIELD

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ABSTRACT

Thirteen new combinations are made in the genus *Eumachia* for species formerly included in the genus *Margaritopsis* and occurring on the Guiana Shield. For these 13 new combinations, their basionyms, other synonyms, types, and distributions are given. Three new combinations are also made for the types of the genera *Chazaliella, Margaritopsis*, and *Readea*, recognized synonyms of *Eumachia*.

KEY WORDS: *Chazaliella, Chytropsis, Margaritopsis*, Guayana Shield, Neotropics, *Readea*, type designations

RESUMEN

Se hacen trece nuevas combinaciones en el género *Eumachia* para especies anteriormente incluidas en el género *Margaritopsis*, que ocurren en el Escudo Guyanés. Los basónimos, otros sinónimos, tipos y distribuciones se presentan para estas trece nuevas combinaciones, se presentan aquí. Se hacen también tres combinaciones nuevas para los tipos de los géneros *Chazaliella*, *Margaritopsis* y *Readea*, sinónimos reconocidos de *Eumachia*.

PALABRAS CLAVES: *Chazaliella, Chytropsis,* denominaciones de tipos, *Margaritopsis*, Escudo Guyanés, Neotropicos, *Readea*

Charles Wright (Sauvalle 1869) published the genus *Margaritopsis* C. Wright with a single species, *M. acuifolia* C. Wright, from eastern Cuba. In the early 20th Century, Urban (1921, 1929) added two more species from Haiti to the genus, *M. lanceifolia* Urb. and *M. triflora* Urb. Until the end of the 20th Century, it was considered to be a small genus, endemic to the Greater Antilles. Andersson (2001, 2002a, 2002b), using molecular phylogenies, demonstrated that *Margaritopsis* is a pantropical genus, with species in the New World and Old World, i.e. Africa, Madagascar, Asia, and the Pacific, and synonymized with *Margaritopsis* two Old World genera, *Chazaliella* E.M.A. Petit & Verdc. and *Readea* Gillespie, and one New World genus, *Chytropsia* Bremek. He estimated that *Margaritopsis* would have approximately 50 species. Taylor (2005) cited 27 species of *Margaritopsis* in the Neotropics, nearly three times as many as Andersson had estimated for the New World, and suggested that there are probably more species of *Margaritopsis* to be discovered there. Barrabé et al. (2012), using molecular and morphological analyses, investigated more Asian, Australasian, and Pacific species, and concluded that more Old World species should be included in *Margaritopsis*, bringing the number of species to more than 70 worldwide. Barrabé and Davis (2013) showed that *Eumachia* DC. is also synonymous with *Margaritopsis*, and has priority over it.

Barrabé and Davis (2013) proposed the conservation of *Margaritopsis* over *Eumachia* because the latter has been either treated as a dubious genus or as a synonym of *Psychotria s.l.* (Robbrecht 1988:240, 1993:186), and only has a single species, *E. carnea* (G. Forst.) DC. *Margaritopsis* was well known among rubiologists, and at least 27 *Margaritopsis* species would have to be transferred to *Eumachia*. The Nomenclature Committee for Vascular Plants felt that "in view of the small historical size of *Margaritopsis* and the fact that many species from Asia and the Pacific, where *Margaritopsis* has not been considered to occur, must change their names in any case, a majority of the Committee were not convinced that application of the principle of priority would substantially reduce stability of nomenclature," and so did not recommend conservation of *Margaritopsis* over *Eumachia* (Applequist 2014). Since it is expected that this recommendation will be upheld by the General Committee, *Eumachia* is the correct name for the combined genus and must be used instead of *Margaritopsis*. There-

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fore, thirteen new combinations are made here for the *Margaritopsis* species occurring on the Guiana Shield (Funk & Berry 2005). These new combinations are needed for the forthcoming rubiaceous treatment in the *Flora of the Guianas*.

SYSTEMATIC TREATMENT

Eumachia DC., Prodr. 4:478. 1830. Type: *E. carnea* (G. Forst.) DC. [Basionym: *Petesia carnea* G. Forst., Fl. Ins. Austr. 10. 1786]

Margaritopsis C. Wright in Sauvalle, Anales Acad. Ci. Méd. Habana 6:146. 1869. Type: *M. acuifolia* C. Wright in Sauvalle, Anales Acad. Ci. Méd. Habana 6:147. 1869. [= *Eumachia acuifolia* (C. Wright) Delprete & J.H. Kirkbr., comb. nov.]

Readea Gillespie, Bernice P. Bishop Mus. Bull. 74:35. 1930. Type: *R. membrancea* Gillespie, Bernice P. Bishop Mus. Bull. 74:35. 1930. [= *Eumachia membranacea* (Gillespie) Delprete & J.H. Kirkbr., comb. nov.]

Chytropsia Bremek., Recueil Trav. Bot. Néerl. 31:291. 1934. *Psychotria* sect. *Chytropsia* (Bremek.) Steyerm., Mem. New York Bot. Gard. 23:484. 1972. Type: *C. astrellantha* (Wernham) Bremek. [= *Eumachia astrellantha* (Wernham) Delprete & J.H. Kirkbr.]

Chazaliella E.M.A. Petit & Verdc., Kew Bull. 30:267. 1975. Type: *C. abrupta* (Hiern) E.M.A. Petit & Verdc. [Basionym: *Psychotria abrupta* Hiern in Oliver, Fl. Trop. Afr. 3:205. 1877; = *Eumachia abrupta* (Hiern) Delprete & J.H. Kirkbr., comb. nov.]

1. Eumachia albert-smithii (Standl.) Delprete & J.H. Kirkbr., comb. nov. *Psychotria albert-smithii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8:203. 1930. *Margaritopsis albert-smithii* (Standl.) C.M. Taylor, Syst. Geogr. Pl. 75:169. 2005. Type: PERU. Loreto: Soledad, on the Río Itaya, 110 m, 20–22 Sep 1929, *E.P. Killip & A.C. Smith 29766* (holotype: F No. 607482; isotypes: fragments G barcode G00300217, NY barcode 00132588, US No. 1463026 [barcode 00138632]).

Distribution.—Widespread in South America.

2. Eumachia astrellantha (Wernham) Delprete & J.H. Kirkbr., comb. nov. *Psychotria astrellantha* Wernham, J. Bot. 52:316. 1914. *Chytropsia astrellantha* (Wernham) Bremek., Recueil Trav. Bot. Néerl. 31:292. 1934. *Margaritopsis astrellantha* (Wernham) L. Andersson, Syst. Geogr. Pl. 72:230. 2002. Type: GUYANA: Potaro River, below Kaieteur Falls, Sep–Oct 1881 (fl), *G.S. Jenman 959* (holotype: K barcode K000173648).

Rudgea obscura Sandw., Bull. Misc. Inform. Kew 1931:474. 1931. Type: GUYANA: Cuyuni River, below Akaio Falls, 22 Nov 1929 (fl, fr), *N.Y. Sandwith 647* (holotype: K barcode K000173646; isotypes: K barcode K000173647, NY barcode 00133225).

Distribution.—Southern Venezuela, Guyana, Suriname, French Guiana, and throughout Brazil.

3. Eumachia boliviana (Standl.) Delprete & J.H. Kirkbr., comb. nov. *Psychotria boliviana* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:302. 1931. *Margaritopsis boliviana* (Standl.) C.M. Taylor, Syst. Geogr. Pl. 75:170. 2005. Type: BOLIVIA. La Paz: San Carlos, region of Mapiri, 850 m, 3 Nov 1926 (fl), *O. Buchtien 1489* (holotype: F No. 609011; isotype: F No. 611732).

Psychotria lawrancei Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 17:281. 1937. Type: COLOMBIA. Boyacá: region of El Humbro, 1050 m, 6 May 1933 (fl), *A.E. Lawrance 788* (holotype: F No. 681079; isotypes: E barcode E00285008, F No. 1525171, G barcode G00300182, G barcode G00300183, MO No. 1068126, S No. 05-1091).

In JSTOR Global Plants (2015) there is a specimen from WIS, barcode 00001028 MAD, with the label "Lawrance 788 – Psychotria lawrancei, new species" and another label "Isotype Psychotria lawrancei Standl." While the specimen label corresponds to that of the holotype, the specimen belongs to the family Lauraceae, and is not an isotype.

Psychotria foetidiflora Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:202. 1940. Type: BRAZIL. Amazonas: Parintins, 22 Dec 1935 (fl), *A. Ducke s.n. (RB 34998)* (holotype: F No. 932981; isotype: K barcode K000173649).

Psychotria kukenanensis Steyerm., Fieldiana, Bot. 28:601. 1953. Type: VENEZUELA. Bolívar: Gran Sabana, Río Kukenán, between waterfall at Rué-Merú (tributary of Río Kukenán) and Divina Pastora, on Río Kukenán N of Santa Helena, S of Mount Roraima, 1065 m, 3 Oct 1944 (fl), *J.A. Steyermark 59227* (holotype: F No. 1181464; isotype: US No. 1908727 [barcode 00138821]).

Psychotria turboensis Standl. ex Steyerm., Acta Bot. Venez. 4:101, fig. 49. 1964. Type: COLOMBIA. Antioquia: N of Dabeiba, on road to Turbo, 350 m, 26 Feb 1942 (fl), *R.D. Metcalf & J. Cuatrecasas 30119* (holotype: F No. 1124872; isotypes: MO No. 1272932, US No. 1833446 [barcode 00146645]).

Psychotria puberulenta Steyerm., Mem. New York Bot. Gard. 23:488. 1972. Type: GUYANA: Pakaraima Mountains, Upper Mazaruni River, Sagaraimadai Savanna, 550 m, 16 Nov 1951 (fl), *B. Maguire & D.B. Fanshawe 32618* (holotype: NY barcode 00132790; isotypes: US No. 3035272 [barcode 00138942], VEN No. 82306).

Psychotria plowmanii Steyerm., Ann. Missouri Bot. Gard. 71:1178. 1984. Type: VENEZUELA. Amazonas: Depto. Atures, along Río Cataniapo, 44–45 km SE of Puerto Ayacucho, 3 km downstream from damsite, 5°35'N, 67°15'W, 200–300 m, 9 May 1980 (fl), *J.A. Steyermark, G. Davidse & F. Guanchez 122132* (holotype: VEN No. 136287; isotype: MO No. 3100818).

Psychotria ronaldii Steyerm., Ann. Missouri Bot. Gard. 74:111, fig. 10. 1987. Type: VENEZUELA. Amazonas: Depto. Atabapo, Cerro Huachamacari, 3°39'N, 65°42'W, 600–750 m, 4 Mar 1985 (fl), *R.L. Liesner 18214* (holotype: MO No. 3327368; isotype: VEN No. 24833).

Distribution.—Colombia, Ecuador, Peru, Bolivia, southern Venezuela, Guyana, Suriname, and French Guiana.

4. Eumachia cephalantha (Müll. Arg.) Delprete & J.H. Kirkbr., comb. nov. *Mapouria cephalantha* Müll.Arg., Flora 59:495, 497. 1876. *Uragoga cephalantha* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2:959. 1891. *Psychotria cephalantha* (Müll. Arg.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11:235. 1936. *Margaritopsis cephalantha* (Müll. Arg.) C.M. Taylor, Syst. Geogr. Pl. 75:171. 2005. Type: BRAZIL. Minas Gerais: in sylvis prope Lagoa Santa, s.d., *J.E.B. Warming s.n.* (lectotype (Andersson 1992:138): C n.v.; isolectotype: F No. 667820).

Mapouria capituliflora Müll. Arg., Flora 59:495, 497. 1876. *Uragoga capituliflora* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2:959. 1891. *Psychotria capituliflora* (Müll. Arg.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11:235. 1936. Type: BRAZIL. Rio de Janeiro: without locality, s.d., *H.W. Schott s.n.* (lectotype, here designated: BR barcode BR0000008257598).

Distribution.—Amazonian Colombia through Peru to Bolivia, and from northern (including Pará) to southern Brazil and Paraguay.

Müller (1876:495, 497), along with the description of *Mapouria capituliflora* Müll. Arg., cited two syntypes, *Schott s.n.* and *Sellow s.n.*, collected in the Brazilian state of Rio de Janeiro. Specimen BR barcode 0000008257598, has a label with "Brasilia, Schott", author unknown, and is here selected as the lectotype of this name.

5. Eumachia deinocalyx (Sandwith) Delprete & J.H. Kirkbr., comb. nov. *Psychotria deinocalyx* Sandwith, Bull. Misc. Inform. Kew 1939:554. 1939. *Margaritopsis deinocalyx* (Sandwith) C.M. Taylor, Syst. Geogr. Pl. 75:172. 2005. Type: GUYANA: Kibihiu Creek, Wiruni River, Berbice River, 9 Feb 1938 (fl), *D.B. Fanshawe 39 (Forest Department of British Guiana 2683)* (holotype: K barcode K000173645).

Distribution.—Southern Venezuela, Guyana, Suriname, French Guiana, and Amazonian Brazil.

6. Eumachia guianensis (Bremek.) Delprete & J.H. Kirkbr., comb. nov. *Chytropsia guianensis* Bremek., Recueil Trav. Bot. Néerl. 31:292. 1934. *Psychotria moroidea* Steyerm. (nom. nov. for *Chytropsia guianensis*), Mem. New York Bot. Gard. 23:485. 1972, non *Psychotria guianensis* (Aubl.) Raeusch. 1797. *Margaritopsis guianensis* (Bremek.) C.M. Taylor, Syst. Geogr. Pl. 75:172. 2005. Type: SURINAME: Emma Range, 600 m, 15 Mar 1922 (fl), *J.W. Gonggrijp & G. Stahel s.n. (B.W. 5667)* (lectotype (Steyermark 1972: 485, first-step; **second-step lectotype, here designated**): U!; isolectotype: BM barcode BM001009040).

Bremekamp (1934:292) cited the types of *Chytropsia guianensis* Bremek. as "Hab. Emma Range, Gonggrijp et Stahel 5667. Upper Nickerie River, Tulleken 451 co-type:" Steyermark (1972:485) cited the type of *Chytropsia guianensis* Bremek. as "Emma Range, Suriname, *Gonggrijp & Stahel 5667.*" Although he did not cite a herbarium, Steyermark's citation is a first-step lectotypification, and the U specimen is here designated as the second-step lectotype of this name.

Distribution.—Guyana, Suriname, French Guiana, and northern Brazil (Amapá, Pará, Mato Grosso).

7. Eumachia kappleri (Miq.) Delprete & J.H. Kirkbr., comb. nov. *Carapichea kappleri* Miq., Stirp. Surinam. Select. 181. 1851. *Uragoga kappleri* (Miq.) Pulle, Enum. Vasc. Pl. Surinam. 446. 1906. *Psychotria kappleri* (Miq.) Müll. Arg. ex Benoist, Bull. Soc. Bot. France 68:140. 1921. *Cephaelis kappleri* (Miq.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4:335. 1929. *Margaritopsis kappleri* (Miq.) C.M. Taylor, Syst. Geogr. Pl. 75:175. 2005. Type: SURINAME: Marowyne River, Sep 1847 (fr), *A. Kappler 1871* (holotype: U!; isotype: G barcode G00300293!, photo-MO).

Distribution.—Costa Rica, Colombia, Venezuela, Guyana, Suriname, French Guiana, and northern and northeastern Brazil.

8. Eumachia microdon (DC.) Delprete & J.H. Kirkbr., comb. nov. *Rondeletia microdon* DC., Prodr. 4: 408. 1830. *Psychotria microdon* (DC.) Urb., Symb. Antill. 9: 539. 1928. *Mapouria microdon* (DC.) Bremek., Recueil Trav. Bot. Néerl. 31:287. 1934. *Margaritopsis microdon* (DC.) C.M. Taylor, Syst. Geogr. Pl. 75:169. 2005. Type: CUBA: La Havana: Without locality, 1825 (fl), *J.A. de la Ossa s.n.* (holotype: G-DC!; isotype: fragments F No. 635330).

Psychotria pinularis Sessé & Moç., Fl. Mex., ed. 2, 57. 1894. Type: PUERTO RICO: "in monticulo Porto de la Aguadilla, s.d., *M. Sessé & J.M. Moçiño s.n.* (lectotype, here designated: MA barcode MA605231).

Psychotria microdon var. *meridionalis* Steyerm., Mem. New York Bot. Gard. 23:446. 1972. Type: VENEZUELA. Carabobo: Hacienda de Cura, near San Joaquín, 480–1200 m, 4 Jul 1916 (fl), *H. Pittier 7911* (holotype: VEN; isotype: F No. 587678).

On MA barcode 605231 there is a handwritten label (author unknown), "S-1 Psychotria annularis [sic], N. Ic. 1338" and a typewritten label, "Herbarium Horti Botanici Matritensis, Plantae Novae Hispaniae a Sessé, Mociño, Castillo et Maldonado lectae (1787-1795-1804)" with a handwritten identification by Standley, "*Psychotria microdon* (DC.) Urban." It is here selected as lectotype of *Psychotria pinularis* Sessé & Moç.

Distribution.—Antilles, Mexico to Peru, Venezuela, and Suriname.

9. Eumachia nana (K. Krause) Delprete & J.H. Kirkbr., comb. nov. *Psychotria nana* K. Krause in Ule, Verh. Bot. Vereins Prov. Brandenburg 50:109. 1908. *Margaritopsis nana* (K. Krause) C.M. Taylor, Syst. Geogr. Pl. 75:175. 2005. Type: BRAZIL. Amazonas: "Rio Juruá superioris, am Juruá Miry" [Upper Rio Juruá, on the Rio Juruá Mirim (affluent)], Aug 1901, *E. Ule 5670* (holotype: B destroyed, photo [F neg. #467]; lectotype, here designated: K barcode K000173644; isolectotypes: F No. 895487, G barcode G00300185, L barcode L0058073).

Psychotria nudiceps Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8:378. 1931. Type: PERU: San Martín: Tarapoto, Alto Río Huallaga, 360–900 m, 21 Feb 1930 (fl), *Ll. Williams 6600* (holotype: F No. 614571; isotypes: G barcode G00300184, S No. 05-1103, US No. 1496734 [barcode 00138889]).

As the type specimen at B was destroyed, Taylor (2005:175) stated "MO holo-; …" Taylor's statement can be interpreted as a lectotypification, but she did not include the expression "here designated." According to article 7.10 of the ICNafp (McNeill et al., 2012), "For purposes of priority (Art. 9.19, 9.20, and 10.5), designation of a type is achieved only if the type is definitely accepted as such by the typifying author, if the type element is clearly indicated by direct citation including the term "type" (typus) or an equivalent, and, on or after 1 January 2001, if the typification statement includes the phrase "designated here" (hic designatus) or an equivalent." Therefore, Taylor's lectotypification is not valid. The specimen at K with barcode K000173644 is here designated as lectotype.

Distribution.—Peru, Bolivia, southern Venezuela (Amazonas, Apures), and Amazonian Brazil (Acre, Rondonia, Amazonas, Pará).

10. Eumachia pallidinervia (Steyerm.) Delprete & J.H. Kirkbr., comb. nov. *Psychotria pallidinervia* Steyerm., Mem. New York Bot. Gard. 23:492, fig. 68. 1972. *Margaritopsis pallidinervia* (Steyerm.) C.M. Taylor, Syst. Geogr. Pl. 75:175. 2005. Type: VENEZUELA. Amazonas: trail between Camp 2 and Camp 3, Río Yatua, Cerro de la Neblina, 500–700 m, 7 Nov 1957 (fl), *B. Maguire, J. Wurdack, & C.K. Maguire 41996* (holotype: NY barcode 00132763; isotypes: COL barcode 000004667, K barcode K000432835, U No. 256671 [barcode U0006229], US No. 2575553 [barcode 00138905], VEN No. 81954).

Distribution.—Southern Venezuela.

11. Eumachia paupertina (Standl. & Steyerm.) Delprete & J.H. Kirkbr., comb. nov. *Psychotria paupertina* Standl. & Steyerm., Fieldiana, Bot. 28:603. 1953. *Margaritopsis paupertina* (Standl. & Steyerm.) C.M. Taylor, Syst. Geogr. Pl. 75:175. 2005. Type: VENEZUELA. Amazonas: Near Base River (Caño Negro), at southeastern base of Cerro Duida, 215 m, 23 Aug 1944 (fl), *J.A. Steyermark 57919* (holotype: F No. 1181470; isotypes: NY barcode 00132773, VEN No. 15878).

Distribution.—Southern Venezuela.

12. Eumachia podocephala (Müll.Arg.) Delprete & J.H. Kirkbr., comb. nov. *Mapouria podocephala* Müll.Arg., Flora 59: 460, 466. 1876. *Psychotria podocephala* (Müll. Arg.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:109. 1930. *Margaritopsis podocephala* (Müll.Arg.) C.M. Taylor, Syst. Geogr. Pl. 75:176. 2005. Type: VENEZUELA. Amazonas: San Carlos do Rio Negro, s.d. [1853–1854], *R. Spruce 3076* (lectotype (Steyermark 1972:490, first-step; **second-step lectotype, here designated**): K barcode K00173642; isolectotypes: G barcode G00300186, K barcodes K000173641 & K000173643, NY barcode 00132228 , P [2 sheets] barcodes P02285223 & P 02428065, W barcode 0014055 n.v. [photo F neg. #31173]).

Cephaelis caruruensis Standl. ex Steyerm., Acta Biol. Venez. 4: 11. 1964. Type: COLOMBIA. Vaupés: Casa Alvarez, Bocas Carurú, 230 m, 26 Sep 1939 (fl), *J. Cuatrecasas 7019* (holotype: US No. 1795039 [barcode 00129800]; isotype: COL No. 15768 [barcode 000004569]).

Taylor (2005: 176) stated "*R. Spruce 3076* [presumably M n.v. lecto-; selected by Steyermark 1972 p. 490; …" Steyermark (1972: 490) cited the type gathering, but did not designate a single specimen as the lectotype. Taylor designated the specimen at M as lectotype, but failed to state "designated here", so her second-step lectotypification is not valid. The specimen K barcode K00173642 is here designated as second-step lectotype because it has three branches, two with complete inflorescences and one with a complete infructescence.

Distribution.—Colombia, Peru, southern Venezuela, and Amazonian Brazil.

13. Eumachia wilhelminensis (Steyerm.) Delprete & J.H. Kirkbr., comb. nov. *Psychotria wilhelminensis* Steyerm., Mem. New York Bot. Gard. 23:487, fig. 67. 1972. *Margaritopsis wilhelminensis* (Steyerm.) C.M. Taylor (as "*Margaritopsis wilhelmensis*"), Syst. Geogr. Pl. 75:176. 2005. Type: SURINAME: 3 km S of Juliana Top, 12 km N of Lucie River, Wilhelmina Gebergte, 3°39'N, 56°32'W, 300 m, 24 Aug 1963 (fl, fr), *H.S. Irwin, G.T. Prance, T.R. Soderstrom & N. Holmgren 55048* (holotype: NY barcode 00132865; isotypes: F No. 1704829, US [2 sheets] Nos. 2579088 & 2575552 [barcodes 00642657 & 00129578], VEN No. 82114).

Distribution.—Suriname and northern Brazil (Pará).

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BOOK NOTICES

Flora of North America Editorial Committee. 2015. **Flora of North America North of Mexico. Vol. 9: Magnoliophyta: Picramniaceae to Rosaceae.** (ISBN-13: 9780195340297, hbk.). Oxford University Press, 198 Madison Avenue, New York, New York 10016, U.S.A. (**Orders:** oup.com/us, 1-800-445-9714). $95.00, 752 pp., 8.5" × 11".

From the publisher: Flora of North America North of Mexico Volume 9: Magnoliophyta: Picramniaceae to Rosaceae includes treatments prepared by 54 authors covering 691 species in 74 genera classified in four families, with the economically important Rosaceae being by far the largest in the volume with 680 species in 68 genera. Descriptions for all of the families, genera, and species are provided, plus occurrence maps for species are included and 28% of the species are illustrated. Keys are included to aid in the identification of genera in families and species within the genera. Volume 9 is the eighteenth volume to be published in the planned 30-volume *Flora of North America North of Mexico* series.

The thirty-volume ongoing publishing project *Flora of North America* is the first comprehensive taxonomic guide to the extraordinary diversity of plant life covering our continent north of Mexico. This groundbreaking scholarly series is a collaborative effort by researchers at more than 30 U.S. and Canadian botanical institutions. The Flora provides revisions of many plant groups and synthesizes the results from studies published in hundreds of research papers of the last three centuries. With beautiful illustrations accompanying many species, *Flora of North America* is concise, easy to use, and indispensable to botanists, conservationists, ecologists, agronomists, foresters, range and land managers, and horticulturists.

Mark Gustafson. 2015. **A Naturalist's Guide to the Texas Hill Country.** (ISBN-13: 978-1-62349-235-9, flexbound). Texas A&M University Press, John H. Lindsey Building, Lewis Street, 4354 TAMU, College Station, Texas 77843-4354, U.S.A. (**Orders:** www.tamupress.com, 1-800-826-8911). $24.95 US, 360 pp., 328 color photos, 3 maps, table, bib., index, 5.5" × 8.5".

From the publisher: In this guide, biologist Mark Gustafson introduces residents and visitors to the history, geology, water resources, plants, and animals found in the nineteen counties occupying the eastern part of the Edwards Plateau, the heart of the Hill Country.

He profiles three hundred of the most common and unique species from all of the major groups of plants and animals: trees, shrubs, wildflowers, cacti, vines, grasses, ferns, fungi, lichens, birds, mammals, reptiles, amphibians, fishes, and invertebrates. Color photographs are included for each species along with a brief description.

He closes with a chapter on significant state parks and natural areas in the region as an invitation to visit and explore the Texas Hill Country.

As large metropolitan areas continue to encroach on the Hill Country, newcomers are moving in and more people are flocking to its many attractions. This guidebook will enrich the appreciation of the region's rich and unique biodiversity and encourage conservation of the natural world encountered.

Mark Gustafson is professor of biology at Texas Lutheran University in Seguin, Texas, where he directs the environmental studies program and specializes in aquatic biology and ecology.

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NEW SPECIES OF ACANTHACEAE FROM ECUADOR

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ABSTRACT

Four new species of Acanthaceae are recognized for Ecuador. They are the following: **Mendoncia hollenbergiae** Wassh., **M. sericea** Leonard ex Wassh., **Dyschoriste ecuadoriana** Wassh., and **Stenostephanus holm-nielsenii** Wassh.

RESUMEN

Se reconocen cuatro nuevas especies de Acanthaceae para Ecuador. Son las siguientes: **Mendoncia hollenbergiae** Wassh., **M. sericea** Leonard ex Wassh., **Dyschoriste ecuadoriana** Wassh., y **Stenostephanus holm-nielsenii** Wassh.

While preparing the Acanthaceae treatment for the *Flora of Ecuador*, I had set aside a number of collections, mostly from Aarhus (AAU) and Gothenburg (GB) which morphologically seemed to differ from the known species of that region. Unfortunately, while vacating my office at US, these collections were misplaced and they only resurfaced after the publication of the treatment last year. Hence, I would like to publish these novelties at this time before returning these loaned collections to their respective institutions.

Mendoncia hollenbergiae Wassh., sp. nov. (**Fig. 1 A–F**). Type: ECUADOR. Napo: Río Napo between Coca (Puerto Francisco de Orellana) and Had. San Carlos, E of Coca, riverside vegetation, ca. 350 m, 9 Nov 1974, *G. Harling & L. Andersson 11854* (holotype: GB).

Differt a *M. sericea* Leonard ex Wassh. foliis parvis; bracteolis oblongis vel parce ovatis; floribus 1–4 axillaribus; corolla alba cum striis violaceis.

Suffrutescent vine; stem terete, older glabrous, younger sparingly puberulent, nodes inflated, internodes to 10 cm long, slightly twisted. Leaves petiolate, the petioles 1.4–2 cm long, glabrous to minutely puberulous, the blades elliptic to narrowly ovate, 11–13 cm long, 4.5–6 cm wide, apex gradually narrowed to an acuminate tip, basally acute to rounded, firm, glabrous or nearly glabrous, mid- and lateral veins (ca. 3 pairs) more prominent on lower surface than on upper. Flowers 1–4 in each axil; pedicels 1–1.5 cm long, densely appressed-pubescent with white trichomes; bracteoles oblong to narrowly ovate, 20–23 mm long, 8–10 mm wide, densely white sericeous-hirsute or appressed pubescent, conspicuously so along mid-vein and margin, reddish-brown and glabrous within, apex rounded or obtuse, slightly and inconspicuously apiculate, base obtuse to rounded; calyx annular, 0.5 mm long; corollas white with violet striae on lower lip and in throat, tubular, 35 mm long, glabrous without, minutely and inconspicouosly puberulous within, the tube curved, 5 mm broad at base, slightly constricted at 10 mm above base, thence distally expanded to 10 mm at mouth, the limb oblique, 12–15 mm in diameter, subequally 5-lobed, the lobes suborbicular, reflexed, 8–8.5 mm long and 6–8 mm wide; stamens attached 13 mm above the base of the corolla tube; filaments are 2 mm long; anthers sagittate, thecae slightly dissimilar, 6 and 4 mm long respectively, thecae basally terminating in a pubescent disk; ovary glabrous; style 30 mm long; stigma minutely bifid. Drupe not seen.

Mendoncia hollenbergiae is morphologically similar to *M. sericea* Leonard ex Wassh. from the provinces of Orellana and Pastaza in Amazonian Ecuador. The new species is distinguished by having leaf blades 11–13 cm long, 4.5–6 cm wide, flowers 1–4 in each axil, bracteoles oblong to narrowly ovate, 20–23 mm long, 8–10 mm wide and corollas white with violet striae on lower lip and in throat, 35 mm long. In contrast, in *M. sericea* the leaf blades are smaller, 7–11.5 cm long, 2.5–4.5 cm wide, flowers several to numerous, forming compact, axil-

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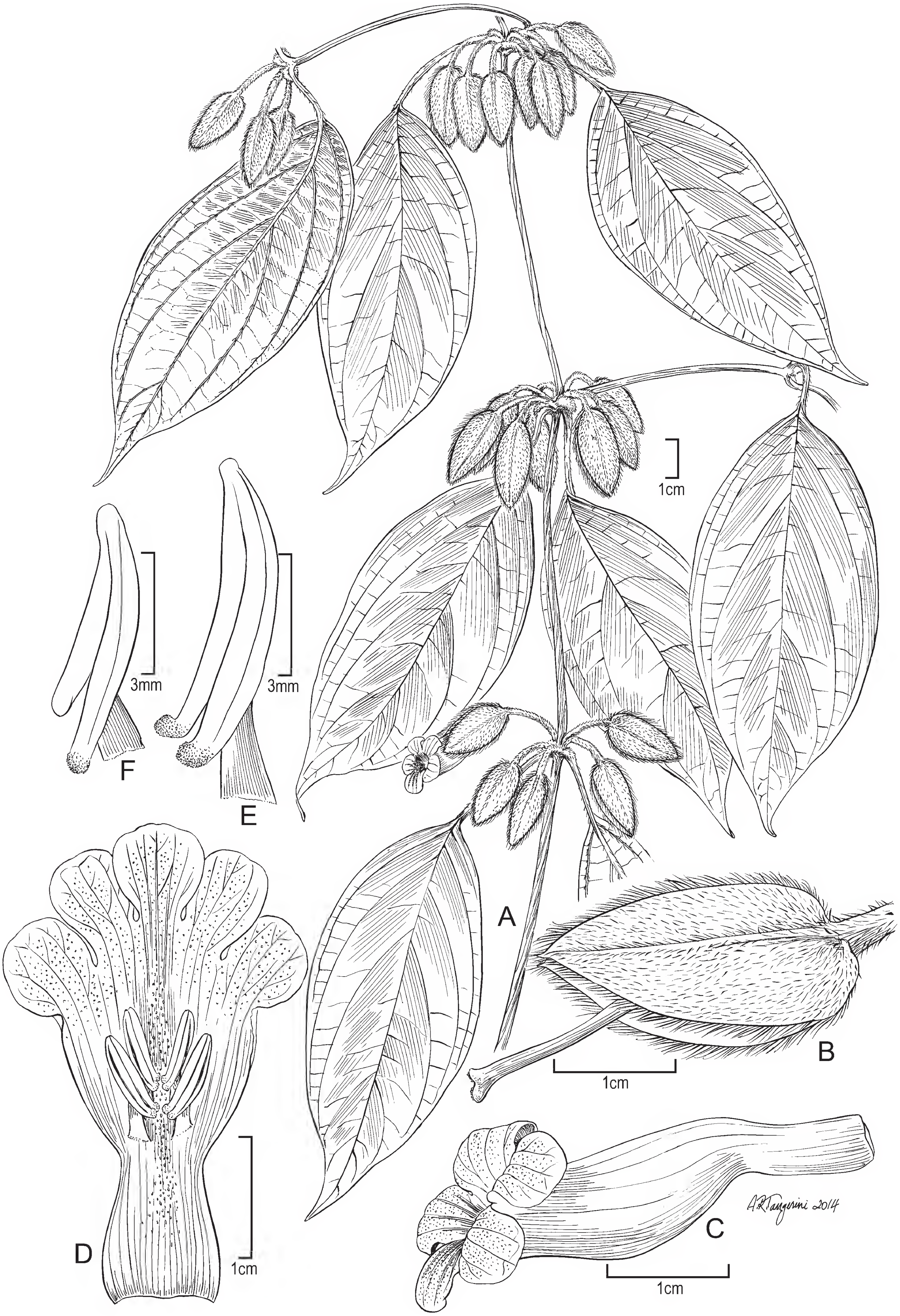
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A.R.Tangerini 2014

Fig. 1. A–F. *Mendoncia hollenbergiae* (*Harling & Andersson 11854*). **A.** Habit. **B.** Bracteoles and pistil. **C.** Corolla. **D.** Corolla expanded and stamens. **E.** Longer pair of stamens and basal pubescent disk. **F.** Shorter pair of stamens and basal pubescent disk.

lary clusters in each axil, bracteoles elliptic to ovate, 10 mm long, 6–8 mm wide and corollas 12–15 mm long, these light green below median lobe.

Distribution.—This species is known only from the type locality.

Etymology.—This name honors Linda A. Hollenberg, whose career was spent in energetic and passionate care of the plant collections in the United States National Herbarium.

Mendoncia sericea Leonard ex Wassh., sp. nov. (**Fig. 2 A–G**). TYPE: ECUADOR. PASTAZA: Mera, in rastrojo, ca. 1100 m, 12 Dec 1955, *Erik Asplund 18815* (HOLOTYPE: S; ISOTYPE: US).

Differt a *M. glomerata* Leonard follis ellipticus vel parce ovatis, firmus, rigidus, glabris; bracteolis ellipticus et anguste ovatis, sericeous; corolla 12–20 mm longa.

Slender, climbing shrub; stem subterete, older glabrous, younger sparingly puberulent, nodes inflated, internodes 4–6 cm long, minutely puberulous. Leaves petiolate, the petioles 2–4.5 cm long, appressed puberulous, the blades elliptic to narrowly ovate, 7–11.5 cm long, 2.5–4.5 cm wide, apex gradually narrowed to an acuminate tip, basally acute to rounded, firm, glabrous or nearly so above, appressed pubescent below, especially on mid- and lateral veins (ca. 3 pairs). Flowers several to numerous, forming compact, axillary clusters; pedicels 1–1.3 cm long, sericeous, the pubescence brownish, appressed and ascending; bracteoles elliptic to narrowly ovate, 10 mm long, 6–8 mm wide, densely and softly sericeous, the trichomes subappressed, whitish to yellowish-brown, conspicuously so along mid-vein and margin, yellowish-brown and glabrous within, apex rounded or obtuse, slightly apiculate, rounded at base. Calyx annular, minute, 0.5 mm long; corollas 12–20 mm long, the tube pale green to white without, essentially reddish-violet within, light green below median lobe, glabrous or subglabrous without, lengthwise minutely puberulous on one half of each lobe within, the tube erect or curved, 5 mm broad at base, slightly constricted at 10 mm above base, thence distally expanded to 7 mm at mouth, the limb oblique, 9 mm in diameter, subequally 5-lobed, the lobes suborbicular, reflexed, 6 mm long and 5 mm wide; stamens attached 6 mm above the base of the corolla tube; filaments are 6 mm long; anthers sagittate, thecae somewhat dissimilar 6 and 4 mm long respectively, thecae basally terminating in a pubescent disk; ovary glabrous; style 10 mm long. Drupe not seen.

Mendoncia sericea is morphologically similar to *M. glomerata* Leonard from the Comisaria of Putumayo, Colombia. The new species is distinguished by having leaf blades elliptic to narrowly ovate, 7–11.5 cm long, 2.5–4.5 cm wide, firm rigid, glabrous or nearly so above, bracteoles elliptic to narrowly ovate and corollas 12–20 mm long. In contrast, plants in *M. glomerata* have leaf blades ovate, 5.5–6.5 cm long, 4–4.5 cm wide, thin, veiny, sparingly strigose or glabrate above, bracteoles ovate and corollas 10 mm long.

Distribution.—Terra firme, in primary humid forest in the provinces of Orellana and Pastaza at elevation of between 200 and 300 meters.

Etymology.—The specific epithet describes the conspicuous sericeous pubescence evident on the bracteoles of the species.

Material studied in addition to the type: **ECUADOR. Orellana:** Parque Nacional Yasuní, km 45 of Maxus Petroleum Road (=YPF), 00°40'S, 76°23'W, 200–300 m, 18 Jan 1998, *Robyn J. Burnham w/Alexander Krings 1549* (MICH); Parque Nacional Yasuní, road construction to Maxus, km 12–16, 00°31'S, 76°32'W, 240 m, 6 Mar 1993, *Jorge Zuleta 194* (US). **Pastaza:** Shiguacocha, ca. 5 km E of Puerto Sarayacu, 1 Oct 1974, *Lugo 3833* (GB, US); Puerto Sarayacu, 30 Oct 1974 *Lugo 3867* (GB, US); Río Zupayacu, ca. 7 km S of Puerto Sarayacu, 11 Oct 1974, *Lugo 4060* (GB, US); Río Capahuari, ca. 12 km N of Puerto Sarayacu, 13 Oct 1974, *Lugo 4137* (GB, US).

Here the author wishes to note that earlier in his career while doing routine identifications of Acanthaceae he determined a number of collections from Ecuador and Peru as "*Mendoncia sericea* Leonard." This was an unpublished name and many of these collections were misidentified. Subsequently these determinations were listed in TROPICOS. In this present study of *M. sericea* Leonard ex Wassh., all of the Ecuadorean material at US was critically examined and cited. No Peruvian collections were examined for this study.

Dyschoriste ecuadoriana Wassh., sp. nov. (**Fig. 3 A–H**). TYPE: ECUADOR. GUAYAS: Nobol, roadside vegetation, 14 May 1974, *G. Harling & L. Andersson 14594* (HOLOTYPE: GB; ISOTYPE: US).

A *D. quitensis* (Kunth) O. Kuntze differt habitu erecti; foliis corollisque parvis et calycibus brevis connatis valde distincta.

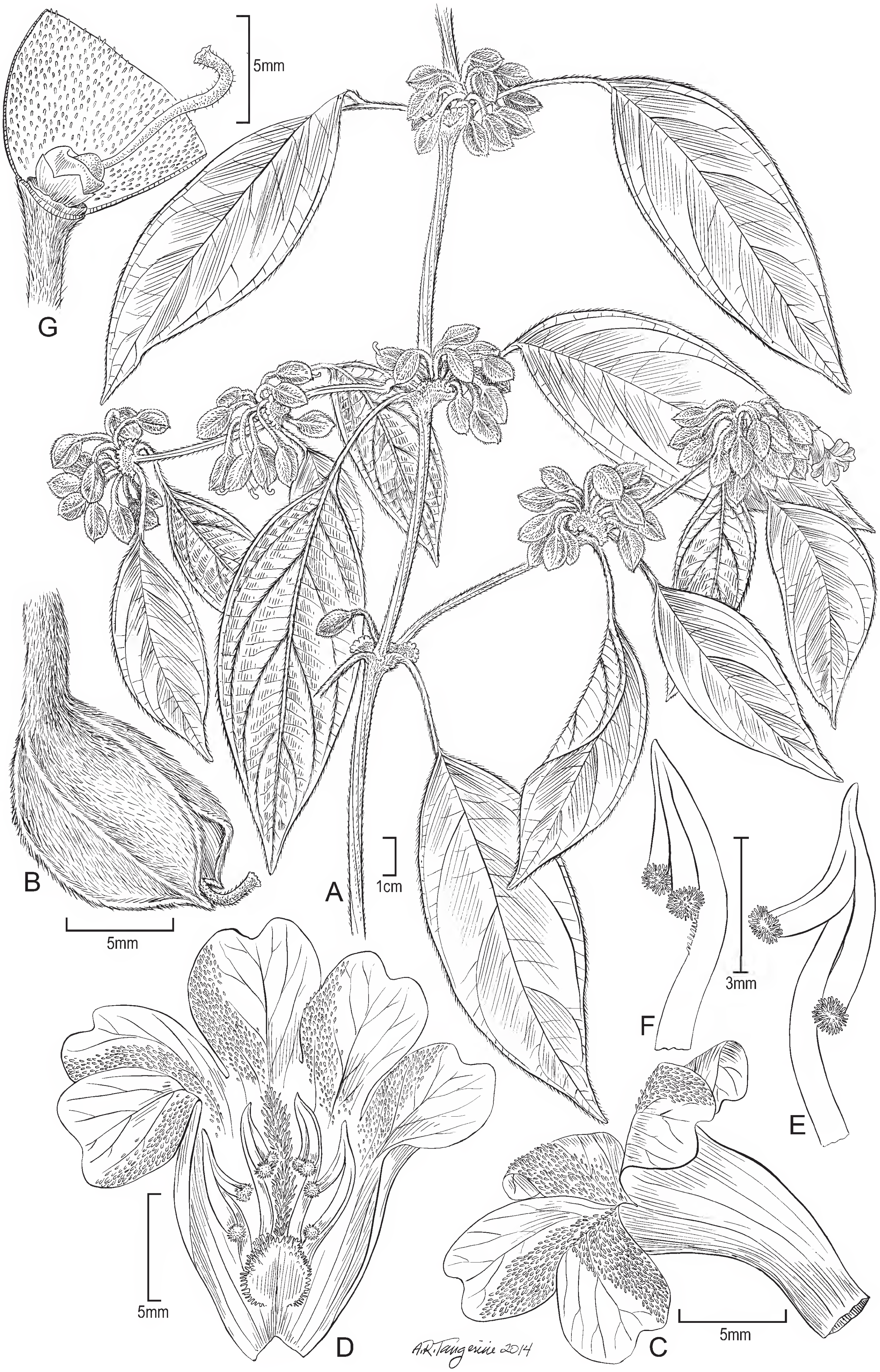
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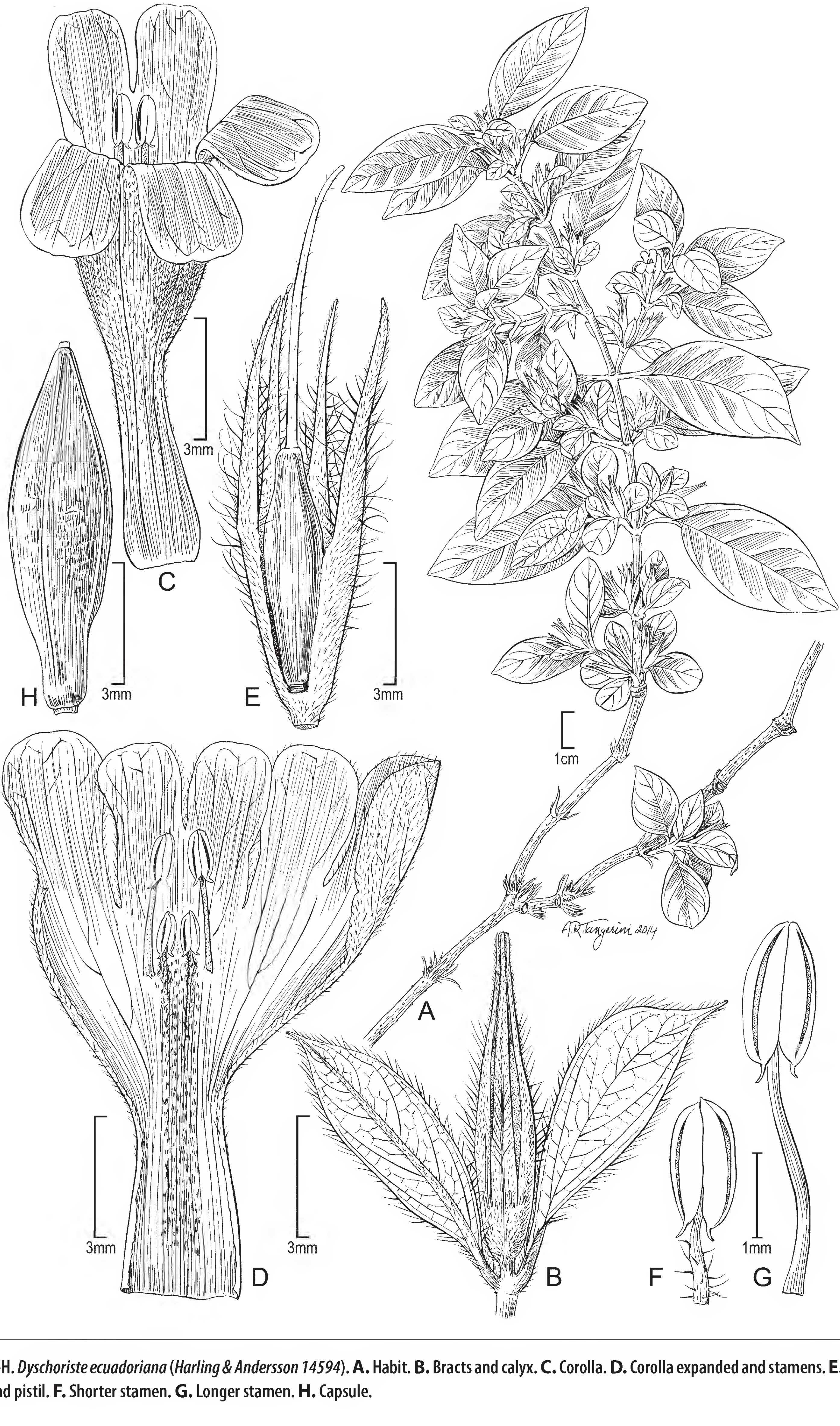
Fig. 2. A–G. *Mendoncia sericea* (*Asplund 18815*). **A.** Habit. **B.** Bracteoles and pistil. **C.** Corolla. **D.** Corolla expanded and stamens. **E.** Longer pair of stamens and basal pubescent disk. **F.** Shorter pair of stamens and basal pubescent disk. **G.** Calyx, nectar disk, ovary, and pistil.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A.R.Tangerini 2014
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Fig. 3. A–H. *Dyschoriste ecuadoriana* (*Harling & Andersson 14594*). **A.** Habit. **B.** Bracts and calyx. **C.** Corolla. **D.** Corolla expanded and stamens. **E.** Calyx, ovary, and pistil. **F.** Shorter stamen. **G.** Longer stamen. **H.** Capsule.

Branched or solitary, erect perennial herbs, from thickened woody base, 30–50 cm tall; young branches subquadrangular, moderately puberulous, older stems subquadrangular, glabrescent. Leaves petiolate, the petioles (unwinged portion) 5–10 mm long, glabrous; the blades ovate to obovate, 4–6.5 × 1.5–3.5 cm, glabrous or nearly so above, sparcely puberulent below, apex obtuse to acute, cuneate and decurrent on the petiole, margin entire, ciliolate; leaves subtending inflorescence reduced, frequently distinctly more ovate and basally rounded rather than cauline leaves. Inflorescence of dichasia in leaf axils, often appearing as glomerules, dichasia opposite or subopposite, 1–3-flowered, sessile to subsessile, peduncles (if present) to 1 mm long; bracts elliptic to oblong, 7.25–8 mm long, 2–2.5 mm wide, glabrous or with a few scattered trichomes, minutely apiculate at apex, margins ciliolate; bracteoles linear, minute, 1.5–2 mm long and 0.1 mm wide. Flowers sessile to subsessile, pedicels to 1 mm long; calyx 12 mm long, the lobes basally fused for about one-third their length, subulate-setaceous, hirsutulous, margins ciliolate; corolla pale violet, 10–12 mm long, sparingly puberulous, tube 9.5–10 mm long, 2 mm broad at base, slightly constricted at 5 mm above base, thence distally expanded to 3.5 mm at mouth, upper lip erect, deeply-bilobed, lobes oblong, rounded, 2.5 mm long and 2 mm wide, lower lip spreading, 3.5 mm long, lobes elliptic, 3 mm long, 2.5 mm wide; stamens inserted just above base of throat, the longer pair 3.5 mm long, the shorter pair 1.5 mm long; longer pair of filaments glabrous, shorter pair hispid; anthers bithecous, thecae equal, 2.5 mm long, distinctly bicalcarate at base; ovay nitid, glabrous, 6 mm high; style 7 mm long, included. Capsule narrowly elliptic to oblong, 9 mm long, 2.25 mm wide, glabrous, obtuse and apiculate; seeds 2–4, oblong, about 2.5 mm long, 1.75 mm wide, notched and oblique at base.

Dyschoriste ecuadoriana is morphologically similar to *D. quitensis* (Kunth) O. Kuntze also from Ecuador and Peru. This new species is distinguished by being a solitary or branched, erect perennial herbs 30–50 cm tall, bracts elliptic to oblong, 7.25–8 mm long and 2–2.5 mm wide, calyx 12 mm long, basally fused for about one-third their length, corollas 10–12 mm long, the tube 9.5–10 mm long and capsules narrowly elliptic to oblong, 9 mm long and 2.25 mm wide. In contrast, *D. quitensis* has plants that are usually procumbent herbs 15–40 cm tall, the bracts are oblong to lanceolate, 8–10 mm long and 2 mm wide, calyx 7–11 mm long basally fused for about one-half their length, corollas smaller, 9–10 mm long, the tube 6.5–7 mm long and capsules narrowly oblong, 7–8 mm long and 2 mm wide.

Distribution.—Along roadsides and in waste places in the provinces of Manabí, Guayas and Loja at elevations between 0 and 1900 meters.

Etymology.—The specific epithet, *D. ecuadoriana,* denotes the western Andean region in which the new species is known to occur.

Material studied in addition to the type: **ECUADOR. Manabí:** Portoviejo-Jipijapa Road, ca. 1 km S of La Pila, ca. 200 m, 4 May 1985, *G. Harling & L. Andersson 24823* (GB, US). **Guayas:** Guayaquil, at golf club, 23–30 Apr 1968, *G. Harling, G. Storm & B. Ström 8803* (GB, US); Isla Puná, May 1892, *Eggers 14741* (US); Oil Camp, between Guayaquil and Salinas, 0–100 m, 21–24 Jun 1923, *A.S. Hitchcock 19998* (US). **Loja:** Road Catacocha-Macará, ca. 8 km S of Empalme, ca. 1900 m, 10 Nov 1977, *G. Harling, U. Eliasson & L. Andersson 15267* (GB); Vilcabamba-Yangana, 1700–1800 m, 15 Apr 1974, *G. Harling & L. Andersson 13594* (GB).

Stenostephanus holm-nielsenii Wassh., sp. nov. (**Fig. 4 A–E**). Type: ECUADOR. Napo: slopes of Guagra Urcu, on the loma above upper Río Borja, SE exposed montane forest, 2600 m, 0°28'S, 77°44'W, 25 Sep 1980, *L. Holm-Nielsen et al. 26982* (holotype: AAU).

Differt a *S. luteynii* (Wassh.) Wassh. foliorum lamina angustata; paniculae floriferae brevis, modice densae; pedicelli longiori; calycis segmenta anguste lanceolata, parce pilosa et minute bulbosa ad apicem, pilis glanduliferis intermixtis.

Suffrutescent plants probably 1–1.5 m tall or more (only tips available for study); stems subquadrangular, reddish, glabrous or the upper portion minutely puberulous, trichomes appressed. Leaves petiolate, the petioles 1.5–5 cm long, moderately puberulous, the blades elliptic to ovate, 9–15 cm long and 3–4.5 cm wide, gradually narrowed to a short-subacuminate tip, cuneate at base, rather thin and membranous, entire or undulate, both surfaces minutely puberulous, lateral veins (6–12 pairs) more conspicuous on lower surface, this also drying a lighter shade of green. Flower-bearing panicles terminal, 7–10 cm long and 5–6 cm broad, compact and moderately dense; mostly sterile cymes axillary to 3 cm long, branches of terminal inflorescence subhelicoid, usually once-forked; bracts subtending branches of inflorescence cordate, 12 mm long, 7.5 mm wide, long-

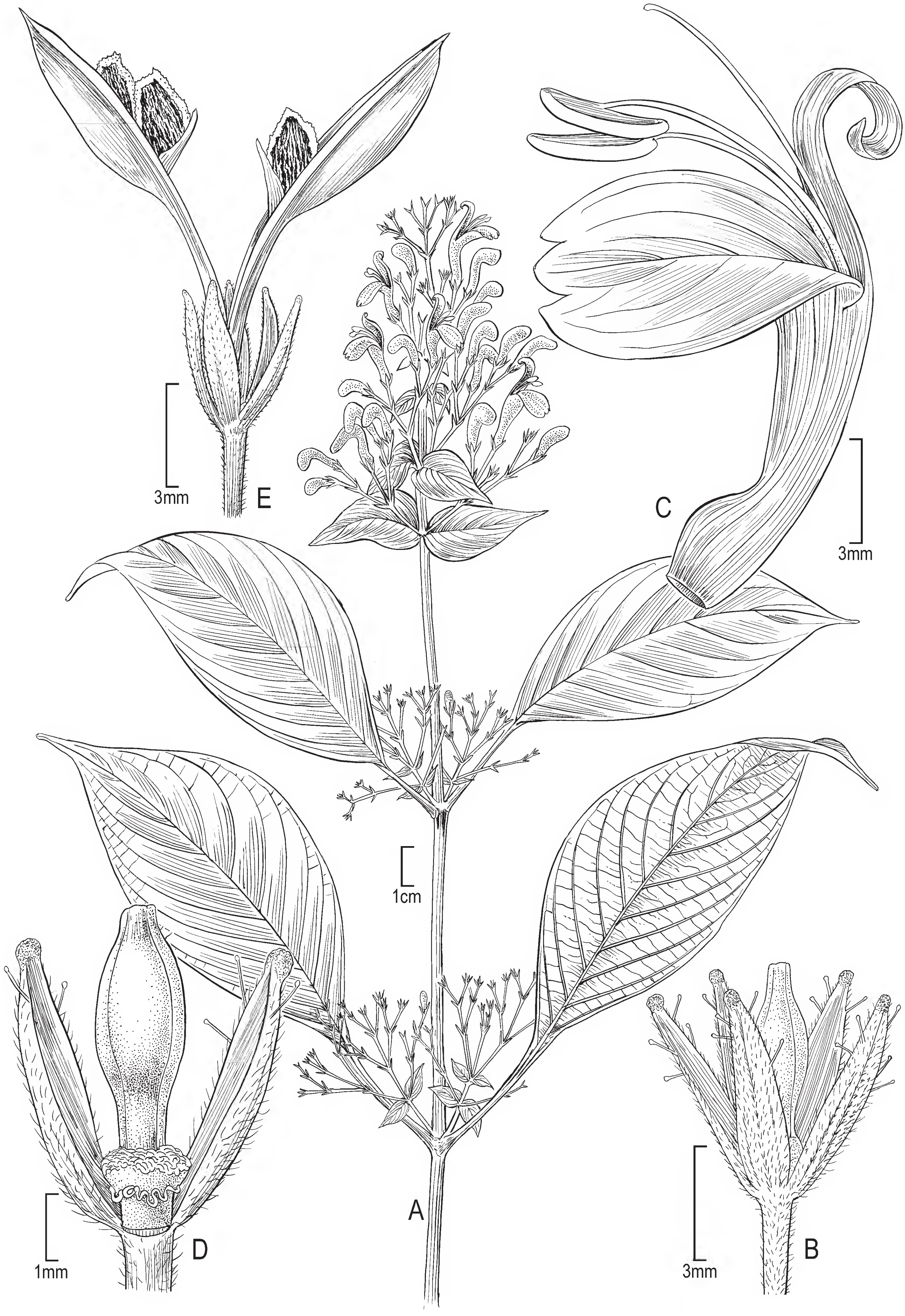

Fig. 4. A–E. *Stenostephanus holm-nielsenii*. A–D: (*Holm-Nielsen et al. 26982*). E: (*Holm-Nielsen et al. 26971*). **A.** Habit. **B.** Calyx and ovary. **C.** Corolla, stamens, and pistil. **D.** Calyx lobes, nectar disk, and ovary. **E.** Calyx lobes, capsule, and seeds.

acuminate at apex, white cystoliths prominent; rachis and rachilla glandular-pilose, trichomes spreading, whitish; pedicels erect, 4 mm long, sparingly glandular-pilose; bracts subtending pedicels green, subulate, 3 × 0.5 mm, sparingly glandular-pilose without; bracts subtending flowers linear, ca. 1.5 mm long, 0.5 mm wide near base, glandular-pilose; calyx 5 mm long, lobes narrowly lanceolate sparingly glandular-pilose, bearing a few acute trichomes to 0.16 mm long on outer and inner surface, especially towards tip, tip itself minutely bulbous, calyces of sterile, lower axillary inflorescence 1–2.5 mm long; corolla wine-red, oblique, 25 mm long from base to tip of upper lip, glabrous, the tube ca. 1.5 mm broad near base, slightly enlarged to 2 mm at 5 mm above base, then geniculate and gradually enlarged to 4 mm at mouth, upper lip erect, 12 mm long, linear-lanceolate, ca. 1 mm wide at base, gradually narrowed to an acute, recurved or curling tip, lower lip spreading, 8 mm long and 6 mm wide, conduplicate, tip 3-lobed, lobes ovate, ca. 1 mm long and wide, obtuse; stamens exserted 4 mm beyond mouth of corolla tube, glabrous, anthers 1–1.5 mm long, densely glandular-pilose, muticous at both ends; style shorter than stamens by about 3 mm, stigma bilobed, lobes minute, rounded; ovary glabrous. Capsule clavate, glabrous, 13 mm long, stipe 5 mm long, head 8 mm long; seeds yellowish, rugose, 2 × 2 mm.

Stenostephanus holm-nielsenii is morphologically similar to *S. luteynii* (Wassh.) Wassh. also from the province of Napo in Ecuador. This new species is distinguished by having narrower leaf blades, these 3–4.5 cm wide, flower-bearing panicles 7–10 cm long, compact and moderately dense, bracts subtending branches of inflorescence long-acuminate at apex, pedicels 4 mm long, calyx lobes narrowly lanceolate, apically sparingly glandualar-pilose and minutely bulbous at tip and the corollas wine-red. In contrast, in *S. luteynii* the leaf blades are broader, 3–5.5 cm wide, the flower-bearing panicles are less dense and compact, shorter, 6–8 cm long, bracts subtending branches of inflorescence rounded and apiculate at apex, pedicels 1–2 mm long, calyx lobes elliptic-oblong, glabrous, subtruncate and apiculate at apex and the corollas deep-maroon.

Distribution.—Montane forest, elfin forest, moist scrub forest at elevations between 2000 and 2900 m.

Etymology.—*Stenostephanus holm-nielsenii* is named after Lauritz Holm-Nielsen of Aarhus University in recognition of the many interesting Acanthaceae he and his team collected during the course of their investigation of plant diversity in Andean Ecuador.

Material studied in addition to the type: **ECUADOR. Napo:** slopes of Guagra Urcu, on the loma above Río Bretania, 0°28'S, 77°41'W, 2000–2200 m, 22 Sep 1980, *L. Holm-Nielsen et al. 26807* (AAU); slopes of Guagra Urcu, on the loma above Río Borja, 0°28'S, 77°44'W, 25 Sep 1980, *L. Holm-Nielsen et al. 26971* (AAU); upper slopes of Guagra Urcu, moist scrub forest, 0°28'S, 77°43'W, 2750 m, 26 Sep 1980, *L. Holm-Nielsen et al. 27183* (AAU); Guara Urcu, the pass between Río Borja and Río Suno, 0°28'S, 77°43'W, 2700 m, 27 Sep 1980, *L. Holm-Nielsen et al. 27274* (AAU); upper Río Suno, near Guagra Urcu, montane forest, 00°28'S, 77°42'W, 2900 m, *L. Holm-Nielsen 27552* (AAU).

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CUATRO NUEVAS ESPECIES Y UN NUEVO REGISTRO DE *FREZIERA* (PENTAPHYLACACEAE) DE ECUADOR Y PERÚ

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RESUMEN

Se describen cuatro especies de *Freziera* (Pentaphylacaceae) nuevas para la ciencia: **Freziera humiriifolia** y **F. yanachagensis** de Ecuador y Perú; y **F. neillii** y **F. tundaymensis** de Ecuador. Se documenta por primera vez **F. carinata** para Ecuador.

ABSTRACT

Four new species of *Freziera* (Pentaphylacaceae) are described as new to science. **Freziera humiriifolia** and **F. yanachagensis** from Ecuador and Peru; and **F. neillii** and **F. tundaymensis** from Ecuador. **Freziera carinata** is documented in Ecuador for the first time.

INTRODUCCIÓN

La familia Pentaphylacaceae contiene 12 géneros y 337 especies alrededor del mundo. En el Neotrópico, está dividida en dos tribus, las cuales constan de cuatro géneros y aproximadamente 127 especies (Every 2009). La tribu Freziereae esta conformada por los géneros *Cleyera* Thunb., *Freziera* Willd., y *Symplococarpon* Airy Shaw; y la tribu Ternstroemieae por el género *Ternstroemia* Mutis ex L.f. (Weitzman et al. 2004). *Freziera* es un género de árboles o arbustos con hojas dísticas y flores funcionalmente dioicas con la corola urceolada, el estilo más corto que el ovario, y el estigma 3–5 lobulado (Weitzman et al. 2004; Every 2009). El género, sin incluir las especies aquí descritas, se encuentra representado por 11 especies en Ecuador (Weitzman 1999) y 12 especies en Perú (van der Werff 1993). Los mismos autores comunican la presencia de otros taxones inéditos para los países mencionados.

Como resultado del estudio de ejemplares depositados en el herbario del Missouri Botanical Garden (MO) y de los especímenes recibidos para identificación en el Gray Herbarium (GH) of Harvard University, se describen cuatro nuevas especies de *Freziera* para Ecuador y Perú. Además se registra por primera vez la presencia de *F. carinata* A.L. Weitzman en Ecuador, que se consideraba endémica de Venezuela, y restringida al Escudo Guyanés en los estados Amazonas y Bolívar (Berry & Weitzman 2005, 2007, 2008).

Las cuatros nuevas especies de *Freziera* aquí descritas son provenientes de las mesetas de arenisca de la Cordillera del Cóndor en Ecuador y hábitats similares en Perú. La Cordillera del Cóndor, compartida entre Ecuador y Perú, es una cadena montañosa ubicada al este de los Andes. Tiene una longitud aproximada de 150 km y una altura máxima de 2900 m. Los suelos están formados principalmente por roca arenisca. Se calcula que la Cordillera del Cóndor tiene una flora de alrededor de 4,000 especies (Schulenberg & Awbrey 1997; Neill 2005; Rodríguez et al. 2006). En los últimos años se han descrito una serie de novedades de la Cordillera del Cóndor que demuestra su alta diversidad (Ulloa & Neill 2006; Clark et al. 2010; Ståhl 2010; Daly et al. 2012; Neill & Asanza 2012; Neill et al. 2012; Riina et al. 2014; Grant 2014). El hallazgo de *Freziera carinata* en la Cordillera del Cóndor demuestra una vez más las afinidades florísticas entre el Escudo Guyanés y esta cordillera, que están separados por más de 3000 km (Ulloa Ulloa & Neill 2006). Otros ejemplos de géneros o especies disyuntos entre esta cordillera y el Escudo Guyanés han sido documentado por Berry et al. (1995) y Neill (2007), incluyendo: *Bonnetia* Mart. (Bonnetiaceae), *Digomphia* Benth. (Bignoniaceae), *Everardia* Ridl. (Cyperaceae), *Phainantha* Gleason (Melastomataceae), *Podocarpus tepuiensis* J. Buchholz & N.E. Gray (Podocarpaceae), *Pterozonium* Fée (Pteridaceae), y *Retiniphyllum tepuiense* Steyerm. (Rubiaceae).

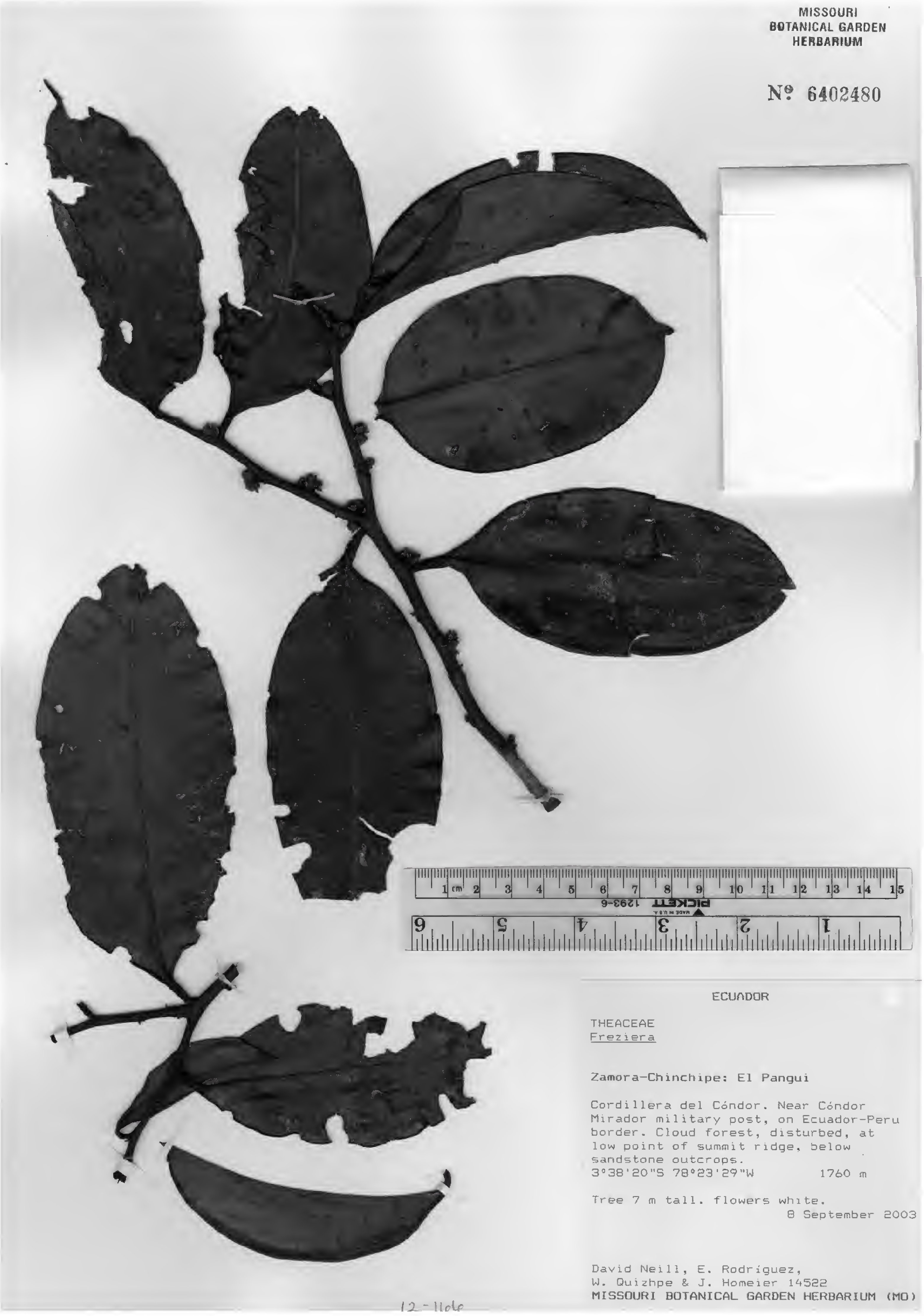
TAXONOMÍA

Freziera humiriifolia D. Santam., sp. nov. (**Fig. 1**). Tipo: ECUADOR. Zamora-Chinchipe: El Pangui, Cordillera del Cóndor, near Cóndor Mirador military post, on Ecuador-Peru border, cloud forest, disturbed, at low point of summit ridge, below sandstone outcrops, 03°38'20"S, 78°23'29"W, 1760 m, 08 set 2003 (fl. ♂), *D.A. Neill, E. Rodríguez, W. Quizhpe, J. Homeier 14522* (holotipo: QCNE-193416 [n.v]; isotipos: GH!, MO-6402480!).

This species is similar to *Freziera dudleyi* and *F. sessiliflora,* but differs from both species in its glabrous branches and large, ovate or oblong-elliptic leaves that are densely pustulate on the upper surface and densely papillate on the lower surface.

Árboles o arbustos 1.5–5[16–18] m o epífita?; **ramas** maduras cilíndricas, la corteza externa negruzca, longitudinalmente estriada, glabras; **ramitas** cilíndricas, glabras, [adpreso pubescentes, los tricomas blanquecinos a amarillento-dorados, 0.3–0.5 mm de longitud], papiladas, sin lenticelas. **Yema terminal** conduplicada, 27–70 mm de longitud, glabrescente, [finamente adpreso o densamente pubescente], los tricomas blanquecinos a amarillento-dorados, 0.5–1.0 mm de longitud. **Hojas** con el pecíolo 0.3–8.0 mm de longitud, caniculado o plano adaxialmente, redondeado abaxialmente, glabro [finamente adpreso pubescentes, los tricomas café rojizo claro, 0.2–0.5 mm de longitud], las alas peciolares presentes o ausentes, si presentes erectas y los márgenes enteros; coléteres ausentes; lámina 7.5–14 × 3.3–6.6 cm, ovada a oblongo-elíptica, la base obtusa, decurrente sobre el pecíolo, generalmente revoluta, ambos lados iguales, el ápice acuminado y con una seta negra y curvada, caduca; margen sinuado, 55–80 dientes por lado, con pequeñas setas insertadas en los senos, uncinadas, negras, caducas, las setas sin tricomas a su alrededor; haz glabro y densamente pustulado; envés glabrescente o adpreso pubescente, los tricomas >0.3 mm [0.5–1.0 mm] de longitud y asociados con papilas, las papilas densas y distribuidas sobre todo la lámina, café-rojizas claras o café-rojizas oscuras a casi negras; nervio central por la haz plano, glabro, densamente pustulado, redondeado en el envés, glabro [adpreso pubescente], papilado-rugoso; nervios laterales 35–60 pares por lado, levemente impresos por la haz y planos en el envés. **Inflorescencias** de 1 flor solitaria, axilar o 3–6 flores fasciculadas, axilares y ramifloras; bráctea 1.0–2.0 × 1.0–2.0 mm, en la base del pedicelo, persistente o caduca, triangular u obovada, generalmente carinada, el ápice agudo, que termina en una seta levemente curvada, caduca, el margen entero, la superficie externa adpreso pubescente, la superficie interna glabra; pedicelo ca. 1.0 mm de longitud o ausente, cilíndrico, erecto, adpreso pubescente; bractéolas 2, 2.0–3.0 × 1.5–2.0 mm, opuestas o subopuestas, levemente desiguales, persistentes, suborbiculares, triangular o en forma de 'D', carinada, la superficie externa finamente adpreso, la superficie interna glabra, el margen ciliado, el ápice redondeado o retuso, terminando en una seta negra, caduca; botones florales 2.5–3.5 mm de ancho; **sépalos** 5, imbricados; sépalos externos 2, 2.5–3.5 × 2.0–3.5 mm, ampliamente ovados a suborbiculares, ápice redondeado y con una seta negra, cónica, la superficie externa adpreso pubescentes, la superficie interna glabra, el margen cartáceo o membranáceo, ciliado y con pequeñas setas café-rojizas en la base o arriba de la base; sépalos internos 3, casi del mismo tamaño y similares en forma a los externos, el ápice redondeado con o sin una seta, adpreso pubescentes en la superficie externa, glabros en la superficie interna, el margen membranáceo, ciliado y con pequeñas setas en toda su longitud, incoloras o sin setas; **pétalos** 5, 2.5–4.5 × 2.5– 4.0 mm, blancos, amarillentos o rojos? (*Wisum 13*), unidos en la base, ovados, glabros, el margen membranáceo y entero, el ápice redondeado o agudo. **Flores estaminadas** con (19–)23–25 estambres, 1.0–2.5 mm de longitud, levemente unidos entre ellos y a la base de los pétalos, ± desiguales; filamentos 0.5–1.5 mm de longitud, levemente aplanados; anteras 0.5–0.9 mm de longitud, obovoides, oblicuas, atenuadas en la base, apiculadas en el ápice; gineceo 2.0–4.0 mm de longitud, más o menos alargado y muy deforme, glabro, 4-locular; estilo separado apicalmente por ca. 1 mm de longitud; estigma 2–4(–5) lobulado. **Flores pistiladas** desconocidas. **Frutos** 4.0–5.0 × [3–]4.0–5.0 mm, oblatos o globosos, verdes y rojos, glabros; paredes del fruto ca. 0.5 mm de grueso; semillas 20–35 por fruto, café-claro o café-negruzcas, brillantes, 1.5–2.0 mm de longitud, de forma no muy definida o más o menos cuneiformes, rugosas o rugoso foveoladas.

Hábitat, distribución y fenología.—Freziera humiriifolia ha sido recolectada en Ecuador en bosques enanos sobre roca arenisca en la Cordillera del Cóndor en las provincias de Morona-Santiago y Zamora-Chinchipe,



ECUADOR

THEACEAE
Freziera

Zamora-Chinchipe: El Pangui

Cordillera del Cóndor. Near Cóndor Mirador military post, on Ecuador-Peru border. Cloud forest, disturbed, at low point of summit ridge, below sandstone outcrops.
3°38'20"S 78°23'29"W 1760 m

Tree 7 m tall. flowers white.
8 September 2003

David Neill, E. Rodríguez,
W. Quizhpe & J. Homeier 14522
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 1. Isotipo de *Freziera humiriifolia* D. Santam. (*D.A. Neill et al. 14522*, MO-6402480).

entre los 1020–1760 m de elevación. En Perú ha sido recolectada en orillas de quebrada en la provincia de Bagua, entre los 320–700 m de elevación. Flores estaminadas han sido recolectadas en setiembre y octubre y frutos en enero, setiembre y diciembre. Lo demás de su fenología se desconoce.

Etimología.—El epíteto específico *humiriifolia* hace referencia a la similitud de las hojas de la nueva especie cuando secas, con las de algunos miembros de la familia Humiriaceae.

Discusión.—*Freziera humiriifolia* se puede distinguir por la siguiente combinación de caracteres morfológicos: ramitas sin lenticelas, hojas cortamente pecioladas, ovadas a oblongo-elípticas, numerosos nervios laterales, levemente impresos por la haz y planos en el envés, densamente pustulados por la haz, la base generalmente revoluta, y el envés glabrescente o adpreso pubescente y densamente cubierto por papilas café-rojizas. También es distintiva por sus inflorescencias sésiles o muy cortamente pediceladas, axilares o axilares y ramifloras y por sus flores con el estilo separado apicalmente. *Freziera humiriifolia* se podría relacionar con *F. sessiliflora* A.H. Gentry, especie muy rara de Colombia y con *F. dudleyi* de Perú y Bolivia. Estas especies comparten hojas cortamente pecioladas, la base revoluta, el margen sinuado, y numerosos nervios no muy conspicuos e inflorescencias axilares o axilares y ramifloras. Para diferencias entre estas especies, véase Tabla 1.

Las dos colecciones aquí citadas de Perú difieren del material típico de Ecuador por ser árboles mucho más grandes y que crecen en elevaciones inferiores. Esas colecciones difieren de las demás por las ramitas, yema terminal, pecíolos y hojas con el indumento más denso y obvio, y los frutos más angostos. Las medidas entre corchetes corresponden a este material. Cuando más material de esta especie se encuentre disponible, será posible determinar si corresponde a un taxón diferente o a variación a través de su ámbito geográfico.

Los signos de pregunta del hábito y coloración de las flores corresponden a la colección *A. Wisum 13* (GH, MO). Es posible que los datos de la etiqueta no correspondan a esta especie.

Especímenes adicionales examinados (paratipos). **ECUADOR. Zamora-Chinchipe:** vicinity of EcuaCorriente copper mine concession, vicinity of mine site, along trail above parking area near end of road, 03°34'54"S, 78°26'06"W, 1330–1360 m, 21 set 2007 (fl. ♂), *T.B. Croat & G. Ferry 98957* (GH, MO, QCNE [n.v]); El Pangui, Cordillera del Cóndor, summit of sandstone plateau of Cordillera, southeast headwaters of Río Wawaime, above proposed EcuaCorriente copper mine area, 03°35'40"S, 78°25'11"W, 1930 m, 08 dic 2005 (fl. ♂), *D.A. Neill & W. Quizhpe 15048* (GH, MO, QCNE [n.v]). **Morona-Santiago:** Limón Indanza, Cordillera del Cóndor, 2 Km al noreste del Centro Shuar Warintza, Meseta de roca arenisca, bosque densos y bajo, 03°09'16"S, 78°14'50"W, 1020 m, 05 oct 2005 (fl. ♂), *A. Wisum 13* (GH, MO); Limón Indanza, Cordillera del Cóndor, Centro Shuar Warints, Cerro Mako Naint a 6 Km del Centro, 03°10'59"S, 78°17'57"W, 1600 m, 07 oct 2002 (fl. ♂), *C. Kajekai 23* (GH, MO, QCNE [n.v]). **PERÚ. Bagua:** Distrito Imaza, Comunidad Aguaruna Putuim, Anexo de Yamayakat, Zonas atlas de Putuim, "campou" 240°SW de Putuim, 700–750 m, 23 ene 1996 (fr), *C. Díaz et al. 7766A* (GH, MO, USM); Región Nororiental del Marañon, Comunidad de Kampaenza, Ribera de la quebrada Shimutaz, río Marañon, 04°55'S, 78°19'W, 320 m, 09 set 1994 (bot. fl. & fr), *N. Jaramillo 433* (GH, MO).

Freziera neillii D. Santam., sp. nov. (**Fig. 2**). Tipo: ECUADOR. Zamora-Chinchipe: Palanda Cantón, Tapichalaca Reserve, S of Podocarpus National Park, E of road between Yangana and Valladolid upper Río Chinchipe watershed, near beginning of mule trail to Quebrada Honda, exposed ridge with very dense montane montane scrub, 04°29'23"S, 79°08'11"W, 2550 m, 14 set 2007 (fl. ♀), *D.A. Neill, C. Davidson & S. Christoph 15999* (holotipo: QCNE-213282 [n.v]; isotipos: GH!, MO-6402471!).

This species differs from *Freziera parva* by the vilose to sericeous abaxial leaf surfaces (vs. glabrous) and 4-locular ovaries (vs. 3-locular).

Árboles o arbustos 3–4 m; **ramas** maduras cilíndricas, la corteza externa negruzca, longitudinalmente estriada, glabras; **ramitas** cilíndricas o muy ligeramente aplanadas, vilosas a esparcidamente vilosas, los tricomas blanquecinos a blanquecino grisáceos, tricomas 0.08–0.1 mm de longitud, papiladas, escasamente lenticeladas, las lenticelas, si presentes, elípticas y blanquecinas. **Yema terminal** conduplicada, 11–25 mm de longitud, densamente hirsuta, los tricomas castaño claro, 0.2–1.0 mm de longitud. **Hojas** con el pecíolo 1.0–3.0 mm de longitud, caniculado adaxialmente, redondeado abaxialmente, glabrescente o cortamente viloso, las alas peciolares presentes o ausentes, si presentes cortas y erectas con los márgenes enteros, los tricomas castaño claros, de 0.5–1.0 mm longitud; coléteres 1, en la base del pecíolo; lámina 3.5–6.1 × 2.7–3.7 cm, oblongo-elíptica, algunas veces más o menos auriculiforme, la base no revoluta, subtruncada a subcordada, algunas veces con un lado asimétrico, el ápice agudo o redondeado y levemente retuso, algunas veces con una seta negra y curvada, caduca; margen crenado, 27–45 dientes por lado, con pequeñas setas insertas en los senos, uncinadas, negras, caducas, generalmente las setas rodeadas de tricomas; haz generalmente glabra, algunas veces diminuta

Tabla 1. Comparación entre algunos caracteres diagnósticos entre *Freziera dudleyi, F. humiriifolia* y *F. sessiliflora.*

Caracteres	*F. humiriifolia*	*F. dudleyi*	*F. sessiliflora*
Indumento en ramitas	Glabras [finamente adpreso]	Seríceas	Densamente pubescentes
Forma de hoja	Ovadas a oblongo elípticas	Angostamente elípticas a casi lineares	Angostamente elíptica
Tamaño de hojas	7.5–14 × 3.3–6.6 cm	7.8–9.3 × 1.2–2.2 cm	7.0–8.2 × 2.3–3.0 cm
Pústulas en el haz	Densas	Ausentes o escasas	Ausentes
Papilas en envés	Densas sobre todo la lámina	Principalmente sobre línea de vernación	Ausentes
Vena media por el haz	Plana	Levemente elevada, vista como una cresta	No observada
Anteras	No moniliformes	Moniliformes	No observadas

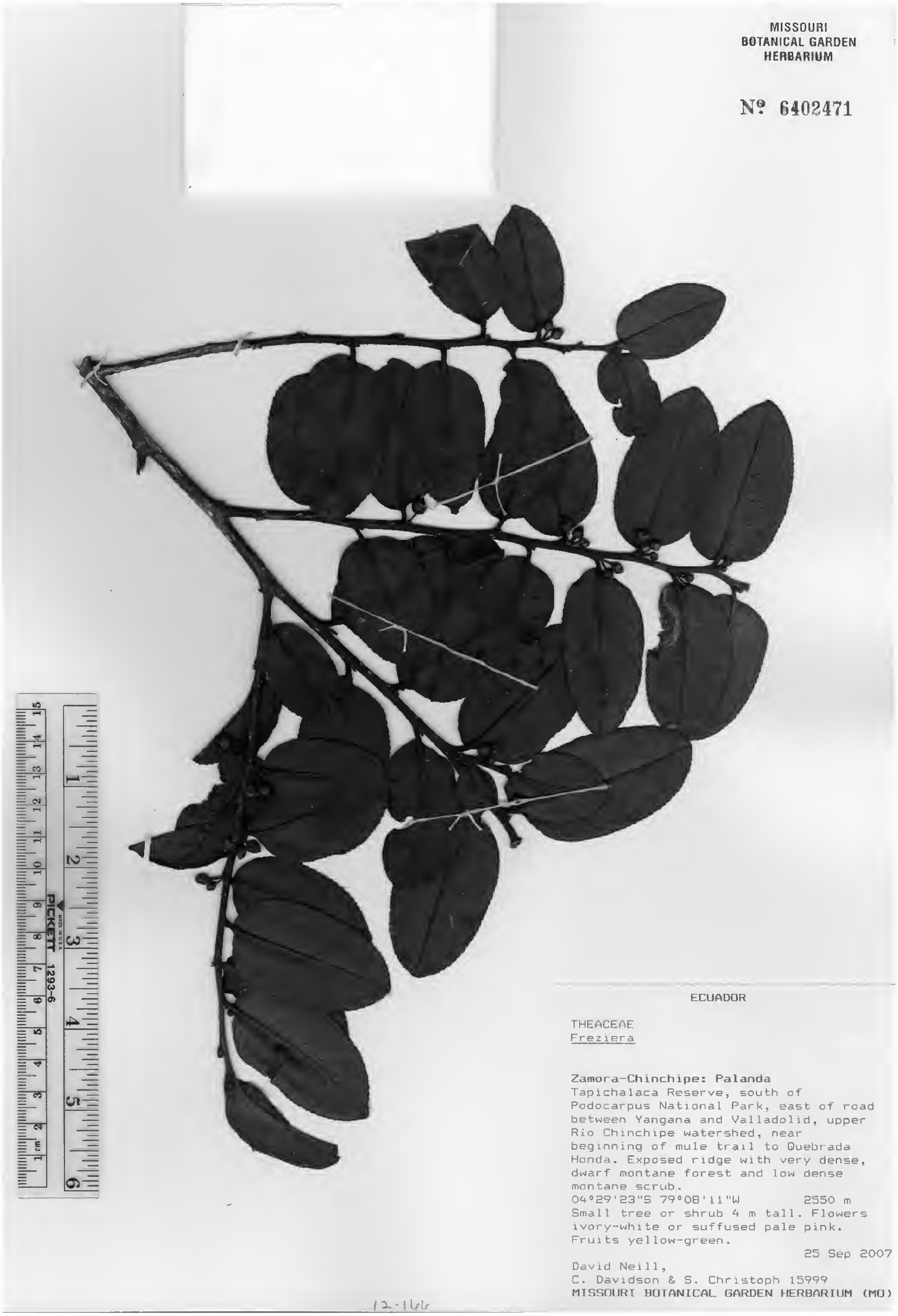
Caracteres entre corchetes [ ] corresponden a las colecciones de Perú.

y muy esparcidamente pubescentes, densamente pustuladas; envés viloso a seríceo, los tricomas 0.5–1.0 mm de longitud y asociados con papilas, las papilas distribuidas sobre todo la lámina, café-rojizas; nervio central por la haz plano o levemente caniculado, glabro o esparcidamente pubescente, densamente papilado; redondeado o triangular en el envés, viloso a seríceo, densamente papilado; nervios laterales 14–27 por lado, impresos en la haz y elevados en el envés. **Inflorescencias** de 1 flor solitaria o 3 flores fasciculadas axilares; bráctea 1.5–3.3 × 0.8–1.5 mm, en la base del pedicelo, persistente o algunas veces caduca, triangular, carinada, el ápice agudo o acuminado, que termina en una seta negra, uncinada, levemente curvada y caduca, el margen entero, la superficie externa adpreso pubescente o glabrescente, la superficie interna glabra; pedicelo 3.0–6.0 mm de longitud, cilíndrico, erecto o alguna veces curvado, glabro; bractéolas 2, 1.5–3.0 × 2.0–3.3 mm, opuestas, levemente desiguales, persistentes, semiorbiculares, generalmente sin una carina, la superficie externa e interna glabras, el margen ciliado, el ápice redondeado y sin una seta negra; botones florales 2.5–4.0 mm de ancho; **sépalos** 5, imbricados; sépalos externos 2, 3.0–4.0 × 3.0–4.0 mm, ampliamente ovados, el ápice redondeado y sin una seta, glabros sobre ambas superficies, el margen membranáceo, esparcidamente ciliado o los cilios ausentes, sin setas en el margen; sépalos internos 3, 3.0–4.0 × 3.0–3.5 mm, iguales a los externos, pero con los cilios en los márgenes generalmente más notorios; **pétalos** 5, 6.0–7.0 × 2.0– 3.0 mm, blancos o blanco-rosados, levemente unidos en la base, lanceolados, glabros, el margen membranáceo y entero, el ápice redondeado o agudo. **Flores estaminadas** desconocidas. **Flores pistiladas** con 17–18 estaminodios (algunas veces los estaminodios ausentes), 0.9–2.5 mm de longitud, unidos a la base de los pétalos, lineares, planos, apiculado en el ápice; gineceo 3.7–4.0 mm de longitud, ovado a cónico, glabro, 4-locular; estilo no separado apicalmente; estigma 4-lobulado. **Frutos** 5.0–6.0 × 3.0–5.0 mm, redondeados, amarillo-verdosos, glabros; paredes del fruto ca. 0.3 mm de grueso; semillas 24–29 por fruto, café rojizas o negras, brillantes, 1.0–1.3 mm de longitud, más o menos cuneiformes o reniformes, foveoladas.

Hábitat, distribución y fenología.—*Freziera neillii* es endémica de Ecuador. Hasta el momento se conoce solo por tres colecciones, todas provenientes de la Reserva Tapichalaca. Ha sido recolectada en bosque montano en la provincia de Loja y Zamora-Chinchipe, entre los 2550–2630 m de elevación. Flores pistiladas y frutos han sido recolectadas de setiembre a noviembre; lo demás de su fenología se desconoce.

Etimología.—El épiteto específico de *F. neillii* es en honor del Dr. David A. Neill (1953–), prolifico botánico estadounidense y experto de la flora ecuatoriana. Él colectó excelentes ejemplares de esta nueva especie. También lideraba el proyecto Inventario Botánico de la Región de la Cordillera del Cóndor, Ecuador-Perú, entre el 2004–2007, durante dicho proyecto se recolectaron varias de las especies aquí descritas.

Discusión.—*Freziera neillii* se puede distinguir fácilmente por varios caracteres en sus láminas foliares: la textura cartácea, el tamaño relativamente pequeño, su forma oblonga-elíptica o algunas veces más o menos auriculiforme, la base subtruncada a subcordada, el ápice agudo o redondeado y levemente retuso, la haz densamente pustulada, el envés viloso a seríceo y densamente papilado, los nervios reticulados, y el margen



MISSOURI
BOTANICAL GARDEN
HERBARIUM

Nº 6402471

ECUADOR

THEACEAE
Freziera

Zamora-Chinchipe: Palanda
Tapichalaca Reserve, south of
Podocarpus National Park, east of road
between Yangana and Valladolid, upper
Río Chinchipe watershed, near
beginning of mule trail to Quebrada
Honda. Exposed ridge with very dense,
dwarf montane forest and low dense
montane scrub.
04°29'23"S 79°08'11"W 2550 m
Small tree or shrub 4 m tall. Flowers
ivory-white or suffused pale pink.
Fruits yellow-green.
25 Sep 2007
David Neill,
C. Davidson & S. Christoph 15999
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

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Fig. 2. Isotipo de *Freziera neillii* D. Santam. (*D.A. Neill et al. 15999*, MO-6402471).

con numerosos dientes y setas rodeadas de tricomas. También es distintiva por sus bractéolas y sépalos relativamente pequeños y completamente glabros (excepto en los márgenes, que son ciliados). Una especie similar a la nueva especie es *Freziera parva* Kobuski, del departamento de Amazonas, Perú. Ambas especies tienen láminas foliares cartáceas, densamente pustuladas en la haz, los nervios reticulados, las setas en el margen de las hojas cubiertas de tricomas y bractéolas y sépalos glabros. *Freziera neillii* se puede diferenciar de *F. parva*, por los caracteres enumerado en la Tabla 2.

Especímenes adicionales examinados (paratipos). **ECUADOR. Loja:** Tapichalaca Reserve, between Yangana and Valladolid, 04°29'S, 79°08'W, 2630 m, 24 oct 2004 (fl. ♀), *J. Homeier et al. 1443* (MO, QCNE [n.v]). **Zamora-Chinchipe**: Palanda Cantón,Tapichalaca Reserve, S of Podocarpus National Park, in upper Río Chinchipe watershed, E of the Yangana-Valladolid road, at the head of the mule trail to Quebrada Honda, 04°29'04"S, 79°07'59"W, 2570 m, 04 dic 2006 (fl. ♀), *D.A. Neill 15361* (GH, MO, QCNE [n.v]).

Freziera tundaymensis D. Santam., sp. nov. (**Fig. 3**). TIPO: ECUADOR. ZAMORA-CHINCHIPE: Cordillera del Cóndor, vertiente occidental, Parroquia Tundayme, Cuenca del Río Tundayme, Camino al destacamento militar Cóndor Mirador, 03°37'15"S, 78°27'20"W, 1260 m, 14 feb 2008 (fl. ♀), *W. Quizhpe, C. Juanga, L. Mayacu 2854* (HOLOTIPO: QCNE-223200 [n.v]; ISOTIPOS: GH!, MO-6402469!).

This species differs from *Freziera smithiana* in its single trichome type (vs. two) and inflorescences of 5–12 flowers (vs. 5–7 flowers).

Árboles 10 m; **ramas** maduras cilíndricas, la corteza externa negruzca, longitudinalmente estriada, glabrescentes; **ramitas** anguladas, velutinas o densamente adpreso pubescentes, los tricomas castaño claros a dorados, ca. 0.5 mm de longitud, sin papilas, escasamente lenticeladas, las lenticelas, si presentes, elípticas o orbiculares, blanquecina-grisáceas. **Yema terminal** conduplicada, 45–55 mm de longitud, densamente pubescente, los tricomas castaño claros a dorados, tricomas 1.0–1.5(–2.3) mm de longitud. **Hojas** con el pecíolo (27–)30–35 mm de longitud, caniculado, redondeado abaxialmente, densamente o esparcidamente pubescente, papilado, las alas peciolares erectas, los márgenes enteros, los tricomas castaño claro a dorados, los tricomas 0.4–1.0 mm longitud y no asociados con papilas; coléteres ausentes; lámina 15–19.8 × 6.0–8.3 cm, elíptica, más o menos falcada, la base no revoluta, con un lado notablemente asimétrico, el lado largo de la lámina obtuso a subtruncado, redondeado a decurrente en lado corto, el ápice acuminado, seta negra no observada; margen sinuado, 35–60 dientes por lado, con pequeñas setas insertas en los senos, curvadas, negras o café rojizas, caducas, las setas rodeadas de tricomas; haz glabra y densamente pustulada; envés lanado, los tricomas 0.5–1.3 mm, sin papilas; nervio central por la haz por ca. 3.5 cm desde la base hacía el ápice caniculado y glabrescente, la parte restante como una cresta elevada de tricomas, sin pústulas; redon deado y densamente pubescente el envés, esparcidamente pustalado, generalmente cubiertas por los tricomas; nervios laterales 45–50 por lado (incluídos algunos intermedios), impresos y levemente surcados por la haz, elevados y redondeados por el envés. **Inflorescencias** de 5–12 flores fasciculadas, axilares o axilares y ramifloras; bráctea 1.0–2.0 × 1.0 mm, en la base del pedicelo, persistente y posiblemente caduca, triangular, aparentemente no carinada, el ápice agudo, la seta en el ápice ausente, el margen entero, la superficie externa pubescente, la superficie interna glabra; pedicelo 0.5–2.0(–4.0) mm de longitud, redondeado, erecto, pubescente; bractéolas 2, 2.0–3.0 × 2.0–2.2 mm, opuestas o subopuestas, levemente desiguales, persistentes, suborbiculares, no carinada, la superficie externa densamente pubescente, glabras en la superficie interna, el margen entero, el ápice redondeado; botones florales 3.0–4.0 mm de ancho; **sépalos** 5, imbricados; sépalos externos 2, 2.8–4.0 × 3.0–3.5 mm, suborbiculares a ampliamente ovados, ápice redondeado y sin una seta negra, superficie externa densamente adpreso pubescentes o el indumento principalmente hacía el centro del sépalo, superficie interna glabra, el margen cartáceo, ciliado, sin setas en el margen; sépalos internos 3, 3.0–4.0 × 3.0, similares en forma a los externos, superficie externa adpreso pubescentes, el indumento menos denso hacía el margen, superficie interna glabra, el ápice redondeado, generalmente quebradizo, el margen membranáceo, sin setas; **pétalos** 5, 4.0–5.2 × 2.5–4.0 mm en botón, amarillos, libres en la base, ovado, glabros, el margen membranáceo-cartáceo, el ápice redondeado o agudo. **Flores estaminadas** desconocidas. **Flores pistiladas** con 17–25 estaminodios, 0.03–0.05 mm de longitud, libres, lineares, planos, agudos en el ápice y con un lado oblicuo; gineceo ca. 3.0 mm de longitud, piriforme, glabro, aparentemente 4-locular; estilo no separado apicalmente; estigma 4-lobulado. **Frutos** 4.0–7.0 × 4.0–5.0 mm, redondeados, de color desconocido, glabros; paredes del fruto ca. 0.3 mm de grueso; semillas ca. 21 por fruto, café rojizas, de forma no muy definida o más o menos cuneiformes, 1.0–1.5 mm de longitud, foveoladas.

Tabla 2. Comparación entre algunos caracteres diagnósticos entre *Freziera neilli* y *F. parva.*

Caracteres	*F. neilli*	*F. parva*
Tamaño de hojas	3.5–6.1 × 2.7–3.7 cm	3.5–4.2 × 1.7–2.1 cm
Indumento en envés	Viloso a seríceo	Glabro, o la pubescencia restringida al nervio central
Longitud de pecíolos	1.0–3.0 mm	5.0–7.0 mm
Base de hoja	Subtruncada a subcordada, algunas veces con un lado asimétrico	Cuneada
Indumento en pedicelo	Glabro	Hirsuto
Número de lóculos	4	3 (según el protólogo)

Hábitat, distribución y fenología.—*Freziera tundaymensis* es endémica de Ecuador, conocida solo por la colección tipo realizada en la región de la Cordillera del Cóndor, en la provincia de Zamora-Chinchipe. Ha sido recolectada en bosque muy húmedo a los 1260 m de elevación. Flores pistiladas y frutos han sido recolectadas en febrero; lo demás de su fenología se desconoce.

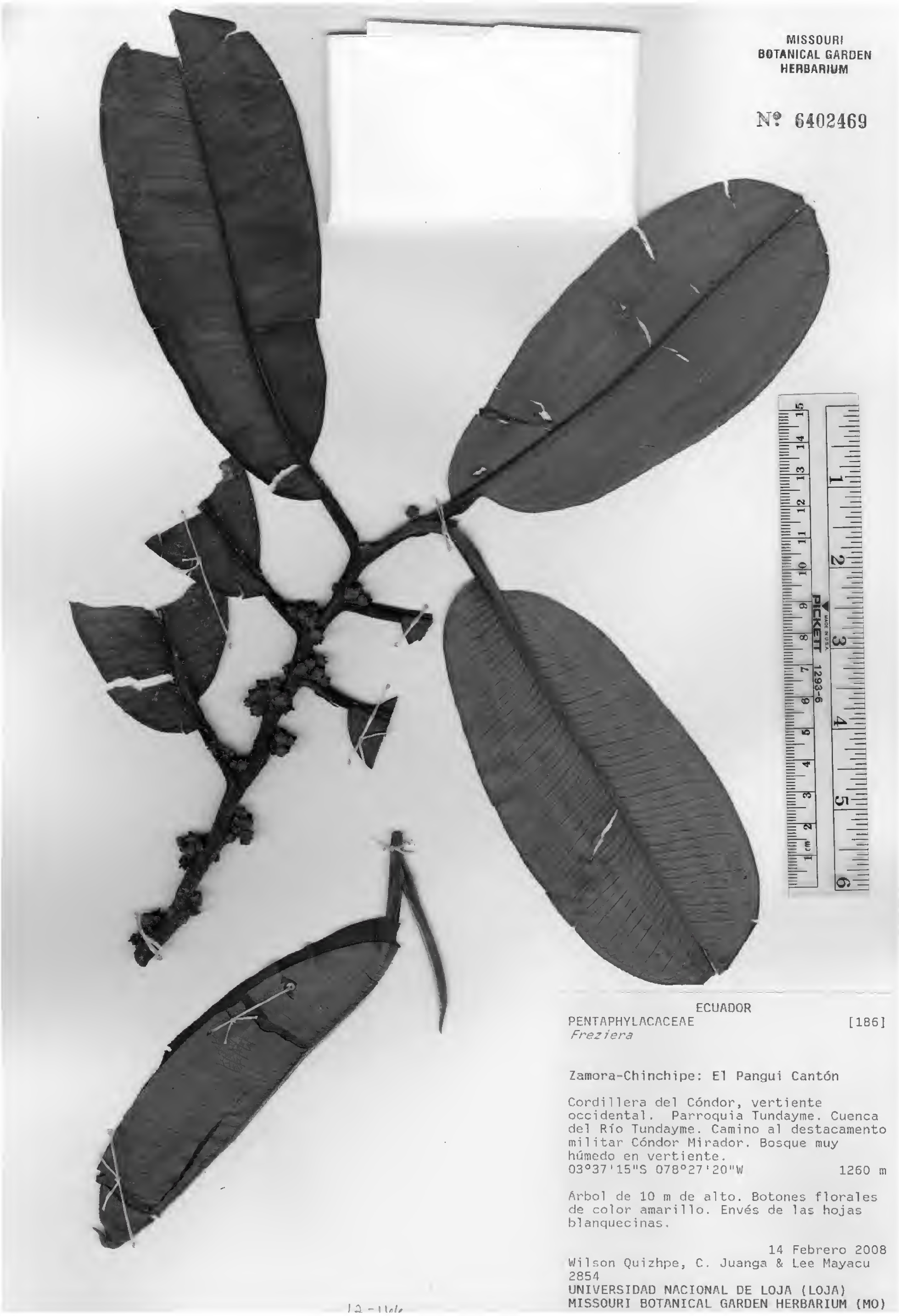
Etimología.—El epíteto específico, *tundaymensis*, hace referencia al río Tundayme, localidad donde fue recolectado el tipo.

Discusión.—*Freziera tundaymensis* se puede distinguir por sus láminas foliares densamente pubescentes en el envés, más o menos falcadas, con la base con un lado asimétrico y numerosos nervios laterales y pecíolos relativamente largos, y por las inflorescencias axilares o axilares y ramifloras con numerosas flores. Esta especie es similar a *Freziera smithiana* Kobuski de Colombia, de la cual se diferencia por tener pecíolos más cortos (vs. 30–40 mm en *F. smithiana*), el nervio central por la haz densamente pubescente, al menos hacía la parte distal (vs. glabro en todo la longitud), y pubescencia de un solo tipo (vs. rizada y recta); además *F. tundaymensis* tiene inflorescencias de 5–12 flores fasciculadas (vs. 5–7 flores fasciculadas). A razón de la base con un lado asimétrico, también podría ser comparada con *F. angulosa* Tul. y *F. inaequilatera* Britton, ambas endémicas de Bolivia, y con *F. forerorum* A.H. Gentry de Panamá. De la primera, se puede diferenciar por sus hojas sésiles o casi así (vs. largamente pecioladas en *F. tundaymensis*). *Freziera inaequilatera* se puede distinguir de *F. tundaymensis* por su indumento ferrugíneo en las ramas, pecíolos, pedicelos y bractéolas (vs. castaño claro a dorados en *F. tundaymensis*), los pecíolos 15–17 mm de longitud (vs. [27–] 30–35 mm), láminas foliares angostas de 4.0–6.0 cm de ancho (vs. 6.0–8.3 cm) y pedicelos de 3.0–4.0 mm de longitud (vs. 0.5–2.0[–4.0] mm). Finalmente, se puede distinguir de *F. forerorum* por sus ramitas glabras y fuertemente anguladas (vs. ramitas velutinas o densamente pubescentes y anguladas en *F. tundaymensis*) y láminas foliares sésiles y estrigosas en el envés (vs. pecioladas y lanadas en el envés).

Freziera yanachagensis D. Santam., sp. nov. (**Fig. 4**). Tipo: PERÚ. Pasco: Oxapampa, Distrito Huancabamba, Parque Nacional Yanachaga-Chemillén, parte alta de la trocha Yanachaga-Palcazú, 10°22'42"S, 75°27'00"W, 2650 m, 01 dic 2007 (fl. ♂), *A. Monteguado, A. Peña, V. Flores & R. Rivera 16076* (holotipo: USM-230940!; isotipos: GH!, MO-6402478!, USM-255371!).

Freziera yanachagensis differs from *F. dudleyi* in having small, elliptic or orbicular leaves with retuse apex and solitary, axillary inflorescences.

Árboles o arbustos 1–6 m; **ramas** maduras cilíndricas, la corteza externa negruzca y con manchas blanquecinas, levemente estriadas longitudinalmente, glabrescentes; **ramitas** cilíndricas, densamente pubescentes, los tricomas blanquecinos a amarillento-dorados, 0.2–1.0(–1.5) mm de longitud, sin papilas, lenticelas ausentes. **Yema terminal** conduplicada, 3.0–5.0 mm de longitud, velutina, los tricomas blanquecinos a amarillento-dorados, 0.4–1.0 mm longitud. **Hojas** con el pecíolo (0.5–)1.0–1.5 mm de longitud, plano o levemente caniculado adaxialmente, redondeado abaxialmente, viloso o glabro, cuando pubescentes los tricomas café rojizos a dorados, tricomas 0.5–1.0 mm de longitud, las alas peciolares ausentes o cortamente aladas, aparentemente sin setas en el margen; coléteres ausentes; lámina 0.5–0.9 × 0.55–0.6 cm, elípticas o orbiculares, la base obtusa a redondeada, igual o levemente desigual, no revoluta, el ápice retuso y con una seta negra y curvada hacía el envés de la lámina, caduca; margen entero en la mitad proximal, sinuado en la mitad distal, 3–6 dientes por lado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Nº 6402469
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ECUADOR
PENTAPHYLACACEAE [186]
Freziera

Zamora-Chinchipe: El Pangui Cantón

Cordillera del Cóndor, vertiente occidental. Parroquia Tundayme. Cuenca del Río Tundayme. Camino al destacamento militar Cóndor Mirador. Bosque muy húmedo en vertiente.
03°37'15"S 078°27'20"W 1260 m

Árbol de 10 m de alto. Botones florales de color amarillo. Envés de las hojas blanquecinas.

14 Febrero 2008
Wilson Quizhpe, C. Juanga & Lee Mayacu
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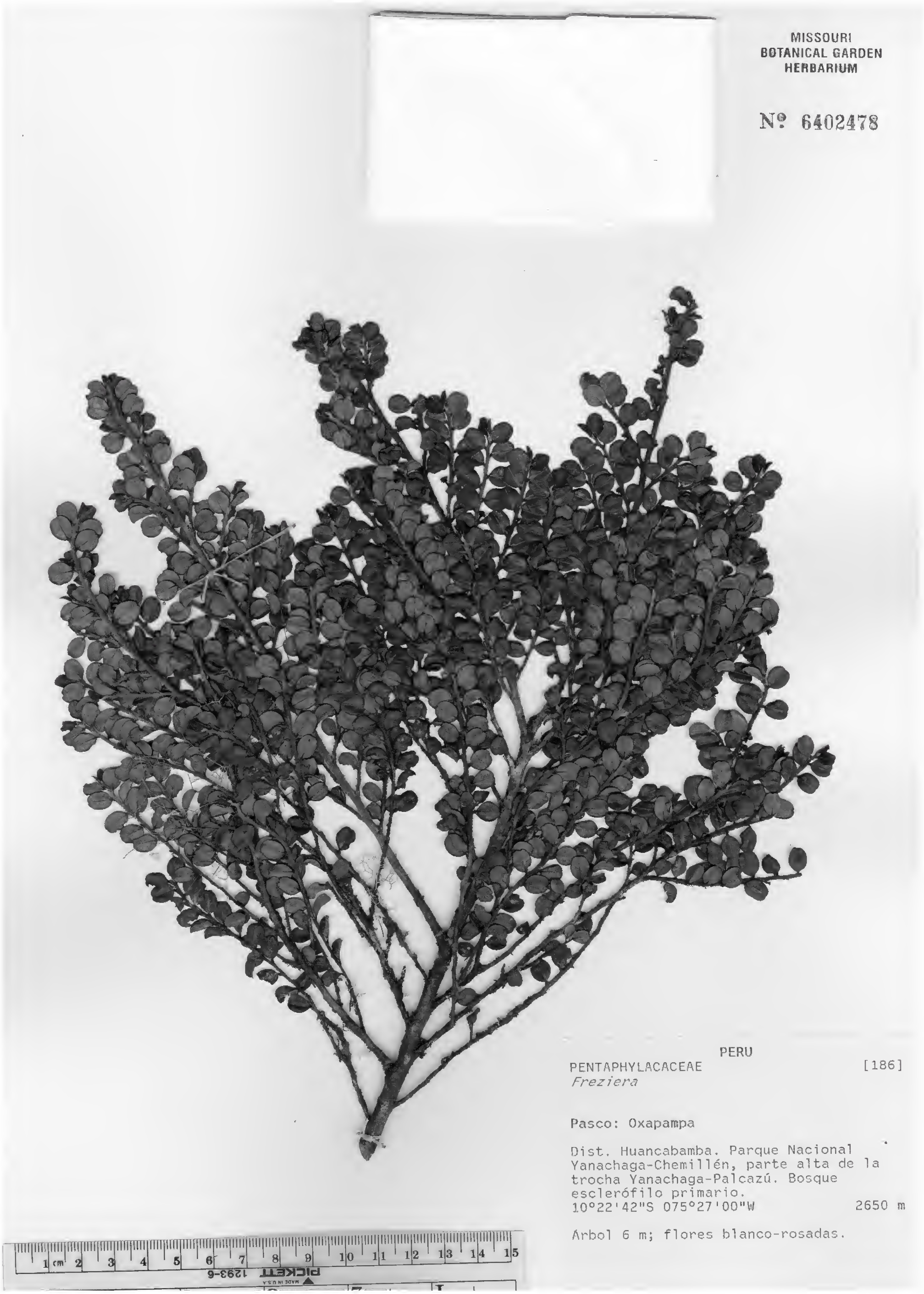
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 3. Isotipo de *Freziera tundaymensis* D. Santam. (*W. Quizhpe et al. 2854*, MO-6402469).



MISSOURI
BOTANICAL GARDEN
HERBARIUM

Nº 6402478

PERU
PENTAPHYLACACEAE [186]
Freziera

Pasco: Oxapampa

Dist. Huancabamba. Parque Nacional Yanachaga-Chemillén, parte alta de la trocha Yanachaga-Palcazú. Bosque esclerófilo primario.
10°22'42"S 075°27'00"W 2650 m

Arbol 6 m; flores blanco-rosadas.

1 cm 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PICKETT 1293-6
MADE IN U.S.A.

FIG. 4. Isotipo de *Freziera yanachagensis* D. Santam. (*A. Monteagudo et al. 16076*, MO-6402478).

(levemente revoluto en toda su longitud), con pequeñas setas insertas en los senos, cónicas o levemente curvadas, negras a café-rojizas, caducas, las setas sin tricomas alrededor; haz glabro, sin pústulas; envés adpreso pubescente, los tricomas 0.8–1.5 mm de longitud y asociados con papilas, las papilas distribuidas sobre todo la lámina, café-rojizas claro o café-rojizas oscuras a casi negras; nervio central por la haz plano o con una pequeña cresta redondeada, glabro, levemente pustulado o las pústulas ausentes; semi-redondeado o aplanado en el envés (algunas veces casi indistinto hacía el ápice), adpreso pubescente, pustulado; nervios laterales 4–6 pares, a menudo muy difíciles de distinguir o ausentes, casi inconspicuos en el envés. **Inflorescencias** de 1 flor solitaria, axilar (algunas veces las flores ocultas bajo las hojas); bráctea 0.8–1.0 × 0.5–1.0 mm, en la base del pedicelo, persistente o caduca, más o menos triangular, carinada, el ápice redondeado o agudo, que termina en una seta cónica, curvada, caduca, el margen ciliado, la superficie externa adpreso pubescente, la superficie interna glabra; pedicelo 0.5–3.2 mm de longitud, cilíndrico, erecto o levemente curvado, glabro, puberulento o adpreso pubescente; bractéolas 2, 0.6–1.0 × 0.7–1.0 mm, subopuestas, desiguales, persistentes, más o menos triangulares o en forma de 'D', no carinada, la superficie externa glabrescente o esparcidamente pubescentes, rugosas, la superficie interna glabra, el margen ciliado, el ápice redondeado y que termina en un seta negra o café-rojiza, caduca; **sépalos** 5, imbricados; sépalos externos 2, 1.2–1.3 × 1.1–2.8 mm, ampliamente ovados o en forma de 'D', ápice redondeado y con una seta negra, cónica, superficie externa glabra o esparcidamente pubescente, superficie interna glabra, margen membranáceo, ciliado, algunas veces con diminutas setas en la base; sépalos internos 3, 1.0–1.3 × 2.0–3.0 mm, iguales a los externos; **pétalos** 5, (1.0–)3.0–3.5 × 2.5–2.8 mm, blancos o blanco-rosados, levemente unidos en la base o libres, ovados o ampliamente ovados, glabros, el margen membranáceo y entero, el ápice obtuso y ligeramente curvado con unos diminutos dientes. **Flores estaminadas** con (6–)10–16 estambres, 1.5–2.5 mm de longitud, libres o levemente unidos a la base de los pétalos, desiguales; filamentos 0.5–1.0 mm, más o menos planos o engrosados; anteras ca. 0.9–1.7 mm, irregularmente moniliformes (no moniliformes en *Montenegro 60*), generalmente ovoides, la base subcordada o truncada, apiculada en el ápice; gineceo 0.7–2.0 mm de longitud, muy deforme o cónico, glabro, 4-locular; estilo separado por ca. 0.5 mm de longitud; estigma 2 o 3 lobulado. **Flores pistiladas** con (5–)10 estaminodios, 0.1–0.7 mm de longitud, libres, lineares, planos, agudos en el ápice; gineceo 0.5–1.0 mm de longitud, redondeado, glabro, 4 o 3?-locular; estilo separado apicalmente por 0.3–0.5 mm de longitud; estigma 2, 3 o 4-lobulado. **Frutos** ca. 2.0 × 2.0 mm, redondeados, de color desconocido, glabros; paredes del fruto ca. 0.2 mm de grueso; semillas desconocidas.

Hábitat, distribución y fenología.—*Freziera yanachagensis* ha sido recolectada en Ecuador y Perú. En Ecuador, se conoce de bosque enano sobre roca arenisca entre los 1930–2000 m de elevación en la Cordillera del Cóndor en la provincia de Zamora-Chinchipe. En Perú, se conoce de bosque primario esclerófilo a los 2650 m de elevación en el Parque Nacional Yanachaga-Chemillén en la provincia de Oxapampa. Flores estaminadas han sido recolectadas en diciembre; flores pistiladas y frutos han sido recolectadas en setiembre. Los frutos de esta especie son poco conocidos; los dos duplicados estudiados tenían pocos frutos y se encontraban agallados. Por esa razón no fue posible observar las semillas.

Etimología.—El epíteto específico hace referencia al Parque Nacional Yanachaga-Chemillén, la localidad donde se recolecto el tipo.

Discusión.—*Freziera yanachagensis* se reconoce fácilmente entre la mayoría de las especies del género por sus partes vegetativas y reproductivas muy pequeñas. También es único en su género por sus hojas que tienen ápice retuso, la venación inconspicua, y el margen levemente revoluto en todo su longitud, entero en la mitad proximal y sinuado en la mitad distal con 3–6 dientes pequeños, los cuales son poco visibles sin el uso de lupa. Además, se caracteriza por tener el envés adpreso pubescente con tricomas asociados con papilas café-rojizas y flores generalmente con las anteras irregularmente moniliformes y el estilo separado apicalmente. A razón de estas dos últimas características se podría comparar con *Freziera dudleyi* A.H. Gentry de Perú y Bolivia y con *F. humiriifolia* aquí descrita. Sin embargo, se puede distinguir por los caracteres enumerados en la Tabla 3. También por tener láminas foliares pequeñas, la nueva especie se podría comparar *Freziera minima* A.L. Weitzman de Ecuador y con *F. stuebelii* (Hieron.) A.L. Weitzman de Colombia, hasta el momento es conocida solamente

TABLA 3. Comparación entre algunos caracteres diagnósticos entre *Freziera yanachagensis*, *F. dudleyi* y *F. humiriifolia*.

Caracteres	*F. yanachagensis*	*F. dudleyi*	*F. humiriifolia*
Forma de la hoja	Elípticas o orbiculares	Angostamente elípticas a casi lineares	Ovadas a oblongo elípticas
Tamaño de las hojas	0.5–0.9 × 0.55–0.6 cm	7.8–9.3 × 1.2–2.2 cm	7.5–14 × 3.3–6.6 cm
Ápice de hoja	Retuso	Acuminado	Acuminado
Inflorescencia	Siempre axilares y solitarias	Axilares y ramifloras de 1–3 flores fasciculadas	Axilares y ramifloras de 3–6 flores fasciculadas

por la fotografía del holotipo (Weitzman, 1987). Al comparar con *F. yanachagensis,* ambas de esas especies tienen láminas foliares más grandes (0.7–1.21 × 0.49–1.4 cm), los márgenes foliares crenados, y los nervios visibles en ambas superficies (más conspicuos, además son bifurcados en *F. stuebelii*). La primera también difiere por sus sépalos externos entre 3.0–3.6 × 2.5–3.3 mm (vs. 1.2–1.3 × 1.1–2.8 mm en *F. yanachagensis*) y por sus frutos más grandes (6.8–7.5 × 5.1–5.5 vs. ca. 2.0 × 2.0 mm). La segunda difiere por sus láminas foliares con la base cordada. *Freziera microphylla* Sandwith y *F. suberosa* Tul. también tienen hojas pequeñas y márgenes foliares con apariencia de no tener dientes y levemente revolutos en todo su longitud, sin embargo en estas dos especies las láminas foliares son elípticas a oblongo-elípticas, entre 1.07–2.8 cm de longitud, el envés densamente seríceas, y con los tricomas amarillos a amarillo-dorados y no relacionados con papilas.

Especímenes adicionales examinados (paratipos). **ECUADOR. Zamora-Chinchipe:** El Pangui, Cordillera del Cóndor, Cresta de la Cordillera, en la frontera Ecuador-Perú, 1 km al sur del destacamento militar Cóndor Mirador, bosque enano, sobre roca arenisca, 03°38'32"S, 78°23'36"W, 2000 m, 16 dic 2000 (fl. ♂), *W. Montenegro & Grupo Post-Grado MO-QCNE 60* (MO, GH); El Pangui, Cordillera del Cóndor, summit of sandstone plateau of Cordillera, SE of headwaters of Río Wawaime, above proposed EcuaCorriente copper mine area, 03°35'40"S, 078°35'40"W, 1930 m, 19 set 2006 (fl. ♀ & fr), *D.A. Neill et al. 15233* (GH, MO, QCNE [n.v]).

NUEVO REGISTRO PARA ECUADOR

Freziera carinata A.L. Weitzman, J. Arnold Arbor. 68 (3):325. 1987. TIPO: VENEZUELA. BOLÍVAR: Auyan-tepui, cumbre de la parte central occidental (división occidental del cerro), vecindad del "Drizzly Camp," sobre piedra de arenisca, a lo largo de afluente del Río Churún, 1760 m, 04 may 1964, *J. Steyermark 93366* (HOLOTIPO: GH!; ISOTIPO: K, NY, U, US, VEN).

Hábitat, distribución y fenología.—Freziera carinata se encuentra en Ecuador y Venezuela. En Ecuador, ocurre en la provincia de Morona-Santiago, donde ha sido recolectada en bosque denso, bosque bajo, y sobre vegetación expuesta en suelo rocoso, entre los 1220–2700 m de elevación. En Ecuador, flores pistiladas han sido recolectadas en diciembre y frutos en octubre; flores estaminadas todavía son desconocidas.

Discusión.—Freziera carinata se reconoce por sus ramitas aplanadas y glabras, pecíolos marcadamente carinados abaxialmente, láminas foliares con el envés denso y diminutamente estrigoso pubescente y con nervio central carinado, la base marcadamente revoluta y por sus flores con las bractéolas y sépalos glabros. *Freziera carinata* en el lenguaje Shuar se le conoce con el nombre común Tsempunim (*A. Wisum 36*).

Algunas colecciones todavía no identificadas del Cerro Golondrinas, Carchi, Ecuador (*Palacios 12505*, MO; *Palacios 12587*, MO; *Boyle et al. 2338*, MO; *Boyle et al. 3410,* MO; y *Bradford 146*, MO) presentan similitudes con *F. carinata*, pero podría representar un nuevo taxón. Ambas poseen ramitas, bractéolas y sépalos glabros y ramitas levemente surcadas. Sin embargo, todo el material mencionado posee láminas foliares un poco más pequeñas (6.2–11 × 3.1–4.1 cm) con el nervio central por la haz redondeado y obviamente pubescente a simple vista, los pedicelos gruesos, y las bractéolas muchas veces más grandes (2.0–)3.5–5.0 mm de longitud que en *F. carinata*.

Especímenes examinados. **ECUADOR. Morona-Santiago:** Limón Indanza, Cordillera del Cóndor, summit ridge of the Cordillera, quartz-bearing igneous rock substrate, headwaters of the Río Warintza, SW of Shuar village of Warints, 03°15'37"S, 78°19'18"W, 2700 m, 16 dic 2002 (fl. ♀ & fr), *D.A. Neill & Grupo Shuar de Conservación 14152* (GH, MO, QCNE [n.v]); Cordillera del Cóndor, Cumbre del Cerro Paatin Naint, 03°13'59"S, 78°16'15"W, 1220 m, 11 oct 2002 (fr), *A. Wisum & Grupo Shuar de Conservación 36* (GH, MO, QCNE [n.v]); Cordillera del Cóndor, Centro Shuar Warints, recorrido desde el Cerro Chankinias hasta la Cordillera del Cóndor, 03°14'41"S, 78°17'29"W, 2200 m, 15 oct 2002 (bot. fl & fr), *A. Wisum & Grupo Shuar de Conservación 55* (GH, MO).

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NEW COMBINATIONS IN *HEXASEPALUM* (RUBIACEAE: SPERMACOCEAE)

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ABSTRACT

Ten new combinations in *Hexasepalum* (Rubiaceae: Spermacoceae) are here proposed, for species formerly in *Diodella*.

RESUMEN

Se proponen diez nuevas combinaciones en *Hexasepalum* (Rubiaceae: Spermacoceae), para las especies anteriormente posicionadas en *Diodella*.

In April of 1913, Small (1913) published the new genus *Diodella* Small, a segregate from the genus *Diodia* L., and transferred one species from *Diodia* to *Diodella*, *Diodella rigida* (Cham. & Schltdl.) Small. He distinguished *Diodella* from *Diodia* by its unbranched styles, capitate or bilobed stigmas, and funnelform corollas versus *Diodia* with branched styles, elongate, slender stigmas, and salverform corollas. In September of the same year, he (Small & Carter 1913) transferred a second *Diodia* species into *Diodella*, *Diodella teres* (Walter) Small. During the following decades, other than Small himself, rubiaceous specialists considered *Diodella* to be synonymous with *Diodia*.

Bacigalupo and Cabral (1999) revised the American species of *Diodia*, and altered the circumscription of *Diodia* from approximately 43 to five species. They consigned 13 species to *Borreria* G. Mey. and nine species to *Galianthe* Griseb., and suggested that 16 *Diodia* species belonged to *Diodella*. Of those 16 species, seven have been reported to be junior synonyms of other *Diodella* species, and three additional species have been added to *Diodella*, which leaves the genus with 12 accepted species at the present time. Bacigalupo and Cabral distinguished *Diodella* by its isomorphic flowers, capitate-bilobed stigmas, fruits consisting of indehiscent mericarps that separate completely and are shed independently at maturity, seeds with an apical, transverse fold, and echinulate pollen. Following the delimitation of *Diodella* proposed by Bacigalupo and Cabral (1999), Delprete published a few new combinations in this genus, in the Rubiaceae treatments of *Flora Ilustrada Catarinense*, *Flora dos Estados de Goiás e Tocantins*, and in a synopsis of the Rubiaceae occurring in the states of Mato Grosso and Mato Grosso do Sul, Brazil (Delprete et al. 2004; Delprete 2010; Delprete & Cortés-B. 2007).

Cabaña Fader et al. (2012) examined the holotype of *Hexasepalum* Bartl. ex DC. and *H. angustifolium* Bartl. ex DC. at PR and discovered that they are synonymous with *Diodella* and *Diodella crassifolia* (Benth.) Borhidi, respectively. Since *Hexasepalum* has priority over *Diodella* this would require the transfer of 11 names now accepted in *Diodella* into *Hexasepalum*. Cabaña Fader et al. (2012) considered, "this would be most disruptive nomenclaturally because the name *Diodella* is, at present, extensively used, while *Hexasepalum* has rarely been mentioned since its publication and generally treated as uncertain". Therefore they proposed that *Hexasepalum* and *H. angustifolium* both be rejected, which would allow the continued use of *Diodella* and its specific names. The members of the Nomenclature Committee for Vascular Plants (Applequist 2013) voted one in favor, 14 against, and three abstentions for rejection of *Hexasepalum* and *H. angustifolium*. The Committee felt "that this is one of those cases in which implementation of the Principle of Priority at the generic level through the adoption of *Hexasepalum* will not cause excessive disruption, so [did] not recommend rejection", and "was not convinced that a change of name for this species would be unusually disruptive, so [did] not recommend the proposal" to reject *H. angustifolium*. This means that it is not possible to use the generic name *Diodella* or its

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specific names. To facilitate their use we are here transferring 10 specific names accepted in *Diodella* to the genus *Hexasepalum*. The name *Diodia teres* Walter was already recently transferred to *Hexasepalum* by Kirkbride (2014).

SYSTEMATIC TREATMENT

Hexasepalum Bartl. ex DC., Prodr. 4:561. 1830. Type: *Hexasepalum angustifolium* Bartl. ex DC.

Diodella Small, Fl. Miami 177. 1913. Type: *Diodella rigida* (Cham. & Schltdl.) Small.

Hexasepalum angustatum (Steyerm.) J.H. Kirkbr. & Delprete, comb. nov. Basionym: *Diodia angustata* Steyerm., Los Angeles County Mus. Contr. Sci. 21:26. 1958; *Diodella angustata* (Steyerm.) E.L. Cabral & Cabaña Fader, Rodriguésia 61(1):120. 2010. Type: BRAZIL. Goiás: Chapada dos Veadeiros, 14 km S of Veadeiros [Alto Paraíso], 14°15'S, 47°30'W, 24 Apr 1956, *E.Y. Dawson 14672* (holotype: R; isotypes: F, LAM, US!).

Distribution.—Endemic to the Chapada dos Veadeiros, Goiás, Brazil.

Hexasepalum angustifolium Bartl. ex DC., Prodr. 4:561. 1830. Type: MEXICO. Hidalgo: Regio-Monte (Real del Monte) Mexicanorum, s.d. [1791–1792], *T.P.X. Haenke s.n.* (holotype: PR; isotypes: G, MO!).

Diodia crassifolia Benth., Bot. Voy. Sulphur 108. 1845; *Diodella crassifolia* (Benth.) Borhidi, Rubiác. México, ed. 1, 185. 2006. Type: MÉXICO. Nayarit: San Blas near Tepic, *G.W. Barklay s.n.* (holotype: BM!).

Distribution.—Endemic to Mexico in the states of Nayarit and Sinaloa.

Hexasepalum apiculatum (Willd.) Delprete & J.H. Kirkbr., comb. nov. Basionym: *Spermacoce apiculata* Willd. in Roem. & Schult., Syst. Veg. 3:531. 1818; *Diodella apiculata* (Willd.) Delprete in A. Reis, Fl. Illustr. Catarinense RUBI, vol. 1:169. 2004. Type: BRAZIL: without locality, s.d. [1804], *F.W. Sieber in Hoffmannsegg s.n.* (holotype, B-W 2626!).

Johann Centurius Graf von Hoffmannsegg never traveled outside of Europe (Lanjouw & Stafleu 1957). Franz Wilhelm Sieber collected for Hoffmannsegg in Pará, Brazil in 1804 (Lanjouw & Stafleu 1957; Vegter 1986), and Hoffmannsegg distributed those specimens with labels bearing only his name. Therefore, Hoffmannsegg's Brazilian exsiccatae were actually collected by F.W. Sieber.

Distribution.—Ranges from Colombia, Venezuela, the Guianas, and Ecuador to Brazil and Paraguay.

Hexasepalum gardneri (K. Schum.) J.H. Kirkbr. & Delprete, comb. nov. Basionym: *Diodia gardneri* K. Schum. in Mart., Fl. bras. 6(6):402. 1889; *Diodella gardneri* (K. Schum.) Bacigalupo & E.L. Cabral, Darwiniana 44:98. 2006. Type: BRAZIL. Ceará: Aracaty, *G. Gardner 1705* (holotype: B†; lectotype, here designated: BM!).

Distribution.—Known from the Brazilian states of Bahia, Ceará, and Piauí.

Hexasepalum lippioides (Griseb.) J.H. Kirkbr. & Delprete, comb. nov. Basionym: *Diodia lippioides* Griseb., Cat. pl. Cub. 141. 1866; *Diodella lippioides* (Griseb.) Borhidi, Acta Bot. Hung. 51:275. 2009. Type: CUBA: *C. Wright 2762* (lectotype, here designated: GOET11312!; syntypes: G, GH, GOET 11313!, K, MO, MPU, NY).

There are two duplicates of *Wright 2762* at GOET, and they appear to be independent gatherings. GOET11312 has a specimen label with Grisebach's handwritten diagnosis, so it is chosen here as lectotype.

Distribution.—Endemic to Cuba.

Hexasepalum mello-barretoi (Standl.) J.H. Kirkbr. & Delprete, comb. nov. Basionym: *Diodia mello-barretoi* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:113. 1940; *Diodella mello-barretoi* (Standl.) Bacigalupo & E.L. Cabral, Darwiniana 44:100. 2006. Types: BRAZIL. Minas Gerais: Municipio Santa Luzia: Serra do Cipó, Km 116, 13 Jan 1934, *H.L. de Mello Barreto 3541* (holotype: F; isotype: BHCB!); 2 Feb 1938, *H.L. de Mello Barreto 9274* (paratype: BHCB!).

Standley (1940) cited an isotype and paratype of *Diodia mello-barretoi* at the Jardim Botânico de Belo Horizonte, Minas Gerais, Brazil. Those specimens were deposited in the Museu de História Natural (BHMH), Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil. The specimens in BHMH were transferred to the Departamento de Botânica (BHCB), Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais where they remain today (pers. comm.: Alexandre Salino 2014).

Distribution.—Apparently endemic to Serra do Cipó, Municipio Santa Luzia, Minas Gerais, Brazil.

Hexasepalum radulum (Willd.) Delprete & J.H. Kirkbr., comb. nov. Basionym: *Spermacoce radula* Willd. in Roem. & Schult., Syst. Veg. 3:531. 1818; *Diodella radula* (Willd.) Delprete in A. Reis, Fl. Illustr. Catarinense RUBI, vol. 1:174. 2004. Type: BRAZIL. Pará: s.d. [1804], *F.W. Sieber in Hoffmannsegg s.n.* (holotype: B-W!).

Distribution.—Widespread in Central and South America; reported from the state of Virginia (USA) in 1959 (Reed 1964), but not persistent.

Hexasepalum rosmarinifolium (Pohl ex DC.) Delprete & J.H. Kirkbr., comb. nov. Basionym: *Diodia rosmarinifolia* Pohl ex DC., Prodr. 4:564. 1830; emend. K. Schum. in Mart., Fl. Bras. 6(6):18. 1888; *Diodella rosmarinifolia* (Pohl ex DC.) Bacigalupo & E.L. Cabral ex Delprete & Cortés-Ballén, Rev. Biol. Neotrop. 3:34. 2006 [2007]. Type: BRAZIL: without locality, s.d., *J.E. Pohl s.n.* (holotype G-DC!).

Distribution.—Occurring in southern Venezuela, and northern and central-western Brazil.

Hexasepalum sarmentosum (Sw.) Delprete & J.H. Kirkbr., comb. nov. Basionym: *Diodia sarmentosa* Sw., Prodr. 30. 1788; *Diodella sarmentosa* (Sw.) Bacigalupo & Cabral, Darwiniana 44:100. [Jul] 2006. Type: JAMAICA: without locality, s.d., *O.P. Swartz s.n.* (syntypes: S S-R-1510!, S S08-117!).

Molecular phylogenetic studies (Dessein 2003; Groeninckx et al. 2009) have suggested that this species is not a member of the genus *Hexasepalum*. Pending further, more definitive phylogenetic studies we are maintaining *H. sarmentosa* in the genus *Hexasepalaum*.

Distribution.—Widespread throughout the Neotropics, in Mexico, Central America, the Antilles, and South America to Bolivia and Brazil; also present in tropical Africa, Malay Peninsula, and Pacific Islands.

Hexasepalum scandens (Sw.) J.H. Kirkbr. & Delprete, comb. nov. Basionym: *Diodia scandens* Sw., Prodr. 30. 1788; *Diodella scandens* (Sw.) Bacigalupo & E.L. Cabral, Darwiniana 44:104. 2006. Type: HISPANIOLA: without locality, s.d., *O.P. Swartz s.n.* (holotype: S S-R-1511!).

Distribution.—Originally endemic to Hispaniola, and currently widespread and naturalized in tropical Africa.

Hexasepalum serrulatum (P. Beauv.) J.H. Kirkbr. & Delprete, comb. nov. Basionym: *Spermacoce serrulata* P. Beauv., Fl. Oware 1:39. 1805; *Dioda serrulata* (P. Beauv.) G. Taylor in A.W. Exell, Cat. Vasc. Pl. S. Tomé 220. 1944; *Diodella serrulata* (P. Beauv.) Borhidi, Rubiác. México, ed. 1, 185. 2006. Type: NIGERIA: Oware, *A.M.F.J. Palisot de Beauvois s.n.* (holotype: G00014459!).

Distribution.—Coastal areas of western Africa, from Senegal to Angola, Macaronesia, southern Mexico to Colombia, and the Antilles.

Hexasepalum teres (Walter) J.H. Kirkbr., J. Bot. Res. Inst. Texas 8(1):17. 2014. Basionym: *Diodia teres* Walter, Fl. carol. 87. 1788; *Diodella teres* (Walter) Small in Small & J.J. Carter, Fl. Lancaster Co. 271. 1913. Type: UNITED STATES. South Carolina: Georgetown Co.: Georgetown, old field, 24 Aug 1939, *R.K. Godfrey & R.M. Tryon 1682* (neotype, designated by Ward (2008: 467): GH00277018!; isoneotypes: NY1163926!, US1838313!).

Distribution.—Its natural distribution is from North to South America and the Antilles. It is introduced and naturalized in the Netherlands, many African countries, China, Japan, and Korea.

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OBSERVATIONS ABOUT *PHASEOLUS LIGNOSUS* (LEGUMINOSAE: PAPILIONOIDEAE: PHASEOLEAE), A BEAN SPECIES FROM THE BERMUDA ISLANDS

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ABSTRACT

This work is the validation of a bean species, *Phaseolus lignosus* Britton, endemic to the Bermuda archipelago. The plant grown out in Colombia from original seed collected on Long Island, Bermuda, matches with the original description. Its morphological characteristics of vegetative parts, raceme, flower and pod, being complete all suggest an affiliation with section *Paniculati* of this genus. An epitype has been designated and distributed since any reference plant material was missing.

RESUMEN

Este trabajo es la validación de una especie de fríjol, *Phaseolus lignosus* Britton, endémica en el archipiélago de Bermuda. Las plantas cultivadas en Colombia a partir de semillas originales colectadas en la isla Long Island de Bermuda, se conforman completamente con la descripción original. Sus características morfológicas de las partes vegetativas, racimo, flor y vaina, ya completamente descritas sugieren una afiliación con la sección *Paniculati* de este género. Se designó y se distribuyó un epitipo por la falta de material vegetal de referencia.

Key Words: wild Bermuda bean, endemic species, Lima bean, type specimen

INTRODUCTION

On February 28, 1918 Nathaniel Lord Britton described *Phaseolus lignosus*, a new bean species, apparently endemic to the Bermuda archipelago (SW North Atlantic Ocean) (Britton 1918, p. 183). This name is acknowledged as valid in the TROPICOS database (Tropicos 2013) and in the USDA germplasm system (Wiersema et al. 1990). It however lacks several morphological details in its description and indications about plant type specimens. For example, Figure 205 is mentioned in the text of the description but with no figure caption in the 'Flora of Bermuda' (op. cit., p. 183), nor any indication that the illustration should be considered as the type, leaving a doubt wheter the author meant something else. The description in effect ends with a bracket "[*P. semierectus* of Reade]" (quoting).

Oswald A. Reade (1883, p. 21), possibly in one of the first plant inventories for that archipelago, described in the non-cultivated *Phaseolus* species, only a *P. semierectus*, with no illustration nor any specimen mentioned. A taxon *P. semierectus* was named by Linnaeus in1767, and listed in the 'Flora Brasiliensis' by Martius (1859–62, p. 189–190) under section *Macroptilium* (and currently it is *Macroptilium lathyroides* var. *semierectum* (L.) Urban (Maréchal et al. 1978)). A careful reading of Reade's description indicates that two legumes are indeed involved in that text: the Bermuda bean of Britton ("stem twining and ascending among trees, etc, ten to twelve feet; leaflets ovate pointed; … habitat, woods near caves (Joyce's)"), and *M. lathyroides* ("pod narrowly cylindrical, three inches long. Distribution West Indies"). About the later, the readership is invited to consult the review by Barbosa-Fevereiro (1986–87, p. 133–136) about morphology and distribution. So, the protologue by Britton includes elements that refer to two different legumes in two different genera, viz. *Phaseolus* L. and *Macroptilium* (Bentham) Urban. This situation possibly explains why this name was still classified as 'unresolved' in the Plant List with data supplied by March 23, 2012 (ThePlantList 2013).

By correcting this caption omission the illustration Fig. 205 (in Britton 1918, p. 183) could serve as a lectotype following the Articles 9.2., 9.3. and 9.11 of the Code (McNeill et al. 2012; Turland 2013). The date of publication of this sketchy figure—after the deadline of 1 January 1908—would question the validity of the

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publication of this taxon along Art. 38.7 and 38.8. of the Code (McNeill et al. 2012; Turland 2013, p. 38 and p. 116). However, along Art. 38.9, an analysis is a figure or group of figures (where one would expect a text!) separate from the main illustration; therefore Art. 38.7 and 38.8 would not apply in this case. On the other hand, by omitting the bracket "[*P. semierectus* of Reade]," a source of confusion would be eliminated, while it seems important to indicate which parts of the original protologue actually apply to the Bermuda bean. For *P. lignosus*, we thus have a description awaiting resolution and a figure (Fig. 205) that constitutes the lectotype.

Lacking a reference plant specimen may be a serious limiting factor in current (e.g. Delgado-Salinas et al. 1999, 2006; López-López et al. 2013) and future phylogenetic studies or any other requiring DNA, as stressed elsewhere (Spencer et al. 2007, p. 17; Turland 2013, p. 71). Incidentally, is the lack of reference plant material the explanation for the absence of *P. lignosus* in most previous reviews of the genus (e.g. Piper 1926; Lackey 1983; Delgado-Salinas 1985; Freytag & Debouck 2002)? The purpose of this note is thus to fill in these missing data in order to further validate this taxon—precisely along the need expressed by the later authors (p. 117)—and to orient future botanical and ecological studies. Three points will be dealt with hereafter: i) the description of a living bean plant received as *P. lignosus* from the Millennium Seed Bank (MSB, Kew, England), ii) the comparison of it with the original description and subsequent validation, and iii) a discussion about findings and relationships with other bean species.

MATERIALS AND METHODS

The plant material used in this study was obtained from MSB under serial number 515078. It is a collection made by C. Watlington (as CW3) in Bermuda, Warwick (not Warick as indicated on the label at K), Cluster Cottage Gardens, on 25 April 2008. This collection is also represented by two original herbarium specimens kept in the Herbarium of the Royal Botanic Gardens, Kew, with bar codes K000650153 and K000650154 (Debouck 2014). The material has been grown in the period April 2013 to August 2014 in closed glass-house at CIAT Palmira, Valle and next in Popayán, Cauca, Colombia (lat. 02° 31' 02.8"N; long. 76° 38' 04.4"W; alt. 1765 masl). Observations were made on living plants in both stations, using calipers and color charts (Royal Horticultural Society (RHS) 1966). Voucher specimens were made out of the living plants by cutting flowering and fruiting stems, and distributed later on to different Herbaria (see under Designation below). Small amounts of seed, accessioned as G40876 (G40876A being the white-flowered variant, see below), can be obtained from the genebank at CIAT (http://www.ciat.cgiar.org/urg). The wild Lima bean, *P. lunatus* L., used in the comparisons is a collection from Santa Ana, El Salvador, Central America (DGD-3236; G27609 in CIAT genebank). As aptly explained by Spencer and co-workers (Spencer et al. 2007, p. 58–59), because there are no genetic alterations (first generation after original collecting, closed growing environment), these cuttings are given a single name under the *Botanical Code* (viz. the Melbourne Code: McNeill et al. 2012) only.

RESULTS

Morphological observations

Plant a pluriannual herbaceous tall indeterminate vine 2–6 m long or more with 8–14 or more axillary inflorescences. **Seedling** 7–12 cm high, from epigeal germination (Fig. 1a). Hypocotyl 20–25 mm, purple (59A; RHS 1966), terete, sparsely covered with minute uncinate hairs. Epicotyl 15 mm, green purple at nodes, terete, glabrous but with few minute uncinate hairs. Eophylls petiolate opposite triangular acuminate cordate at base, glabrous, central vein prominent; the blade 47–55×33–42 mm; the petiole terete canaliculate 28–33 mm long, purplish (60A) with green pulvini; stipules entire or divided rectangular blunt at apex 1×1 mm. First true leaf trifoliolate; terminal leaflet 53–65×32–37 mm, lateral leaflet 44–56×24–32 mm, petiole 36–43 mm, rachis 12–13 mm. **Root** herbaceous fibrous superficial for three months after germination then much ramified, base turning thickened while ageing diam. 5 mm, up to 1 m long and more. **Stems** terete green with purplish dots at nodes, glabrescent with short 1 mm sparsely distributed hairs and minute uncinate hairs mostly found at nodes (Fig. 1b); internodes 102–121 mm long 3–6 mm diam.; sprawling from the 3–4 lower nodes on main stem; climbing from the upper nodes on main stem; after four months 3 m and more long; first internodes pro-

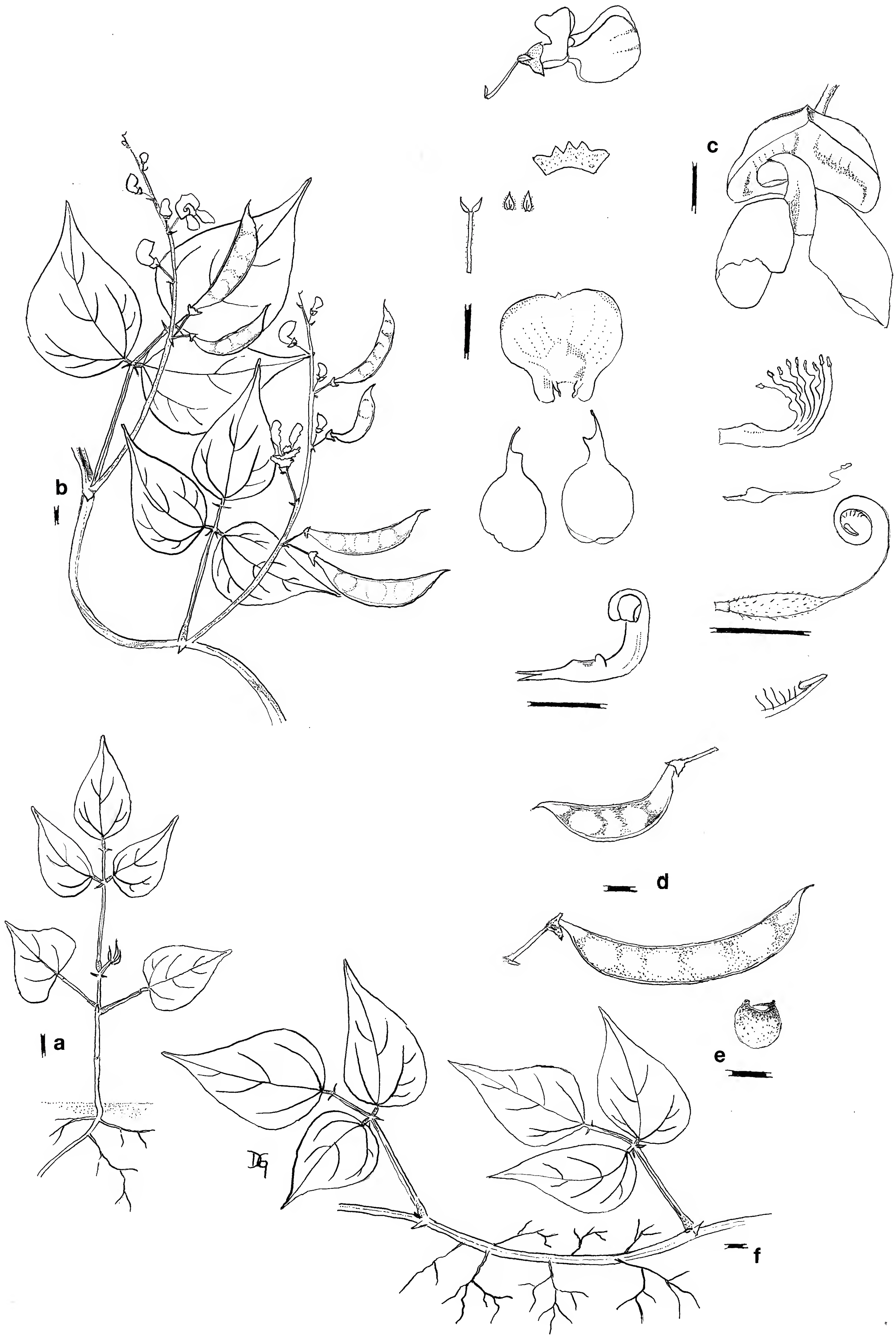

Fig. 1. Drawing of *Phaseolus lignosus* Britton; **a:** seedling; **b:** flowering stem; **c:** flower; **d:** pod; **e:** seed; **f:** rooting internode. Scale bar: 5 mm.

ducing numerous adventicious roots if in contact with soil (Fig. 2 top left); first internodes becoming woody after one year. Stipules triangular lanceolate, spreading horizontally, green glabrous basifix multiveined 3×1 mm. **Leaves** trifoliolate (Fig. 1b) alternate in distichous succession, leaflets ovate rounded at base lengthily acuminate entire lustrous glabrous with minute trichomes, lamina green 141A, main veins prominent beneath turning light purplish with age, terminal leaflets symmetrical 76–90 mm long 53–59 mm wide, lateral leaflets asymmetrical 67–83 mm long 47–53 mm wide. Petiole terete canaliculate 58–107 mm long 1.5–2 mm diam., green sometimes with fine linearly distributed reddish (59A) dots, sparsely covered with short white hairs and minute uncinate hairs. Rachis terete canaliculate green 15–20 mm long 1–1.2 mm diam.. Proximal and distal pulvini green 3.5–5 mm long. Stipels narrowly triangular linear 1.5–2 mm long. **Inflorescence** a pseudoraceme (Fig. 1b; Fig. 2 lower part), ascending, appearing as a compact pyramidal cluster of floral buds intermixed with bracts (9 mm high when peduncle is 20 mm long) (Fig. 2 top right). Peduncle at flowering 45–53 mm long diam. 1.5–2 mm, curved or straight at base, terete, green with basal part towards first insertion turning purplish 61A. Rachis erect or still curved, terete, green, 75–175 mm, with 8–17 floral insertions. Peduncle and rachis glabrous with minute uncinate hairs (more densely covered in upper part of rachis). Primary bracts lanceolate, 2–3 mm long 2 mm wide, green, 3(5)-nerved margin ciliate. Pedicelar bracts narrowly triangular 1-nerved, 1 mm long, green. Pedicel terete, purple, 7–12 mm long 1 mm diam., with minute uncinate hairs (Fig. 3c). Anthesis sequence in secondary raceme was as follows: flower 2 one more day after flower 1, flower 3 four days after, flower 4 six days, and flower 5 (if not falling) eight days. **Flower** papilionaceous asymmetrical (Fig. 1c, Fig. 3a, Fig. 5 left). Bracteoles lanceolate, 2×1.5 mm up to 60% calyx length, greenish, 3(5)-nerved, margin ciliate, central vein prominent, persistent up to one day after anthesis. Calyx cupped, finely reddish speckled, sparsely covered with short white hairs and trichomes, tube 3 mm long, two upper lobes almost united obtuse, three lower lobes subequal triangular 1 mm long 1–1.5 mm wide. Standard broadly half circular markedly reflexed backwards at anthesis (Fig. 3c), external face glabrous cream with a greenish cast (145B) and fine purple veining, internal face glabrous deep purple (72C) with two light magenta rose dots and fine magenta veining, hooded over the keel, 3 mm long to point of flexure then 6 mm to upper margin, 11–12 mm wide, upper margin obtuse-angled, tip slightly pointed, lateral edges unconspicuous, auricles 2–4 mm long, claw 2 mm long whitish with erect narrow parallel callosities, flexure internally thickened. In white-flowered variant (Fig. 5 right) external face pale green (142D). Wings glabrous, magenta (70B-67B) on anthesis fading light purple (75A) the next day, parallel and forward spreading almost horizontally (Fig. 3a), the blade rounded cupped 12 mm long 10 mm wide, left wing 1 mm larger in both directions, outward margin often irregularly undulate, spur right-angled greenish adhering to the keel, claws white linear 3–3.5 mm long. In the white-flowered variant wings pure white on anthesis fading cream yellow (13A) the next day. Keel tubular asymmetrical, greenish white at base pink purple in median part, with two close coils counterclockwise (facing the keel) with a diam. of 3 mm, the terminal coil with a diam. of 2 mm, tube 5 mm long 2 mm wide to first curvature then 4 mm to the coils, terminal coil golden green. Stamens diadelphous (9+1), staminal tube white delicately veined 11 mm long ending into 9 free stamens 5 mm long, vexillar stamen white in free space of staminal tube and on top of dorsal suture of ovary, claw terete 2 mm long with fusiform slightly unequal knob diam. 1.5 mm then 14 mm long, anthers yellow oval dithecal dorsifixed. Ovary green finely puberulent 4 mm long 1 mm wide, laterally compressed, 4–6 ovules, inserted on a yellowish veined basal disk 2 mm long. Style 15 mm long terete coiled with 1.5 close coil at tip, covered by a short white pubescence then glabrous, ending with a loose brush of white hairs in the last 2 mm below the terminal stigma; stigma internal narrow triangular 0.5 mm long. **Pod** laterally compressed (Fig. 1d, Fig. 4a), usually 1–4 seeded (if one, only distal or near distal seed develops); young pod green puberulent curved 18 mm long 3.8 mm wide; when mature 52–55 mm long 9–10 mm wide 7 mm thick, both sutures finely marked, green drying tan, puberulent with very small white hairs; curvature smooth when all embryos develop, scimitar-like when 1–2 embryos develop; base of pod shortly stipitate 3 mm long; pod beak 3.5 mm long delicately curved; spiral twisting of pod valves at dehiscence. **Seed** oblong rounded slightly rhomboid, 8 mm long 5.5 mm wide 4.5 mm thick (Fig. 1e, Fig. 4c), 8.2 g/ 100 seed, tan or grey finely black speckled ending into a black circle around the hilum, hilum 2 mm white sunken.

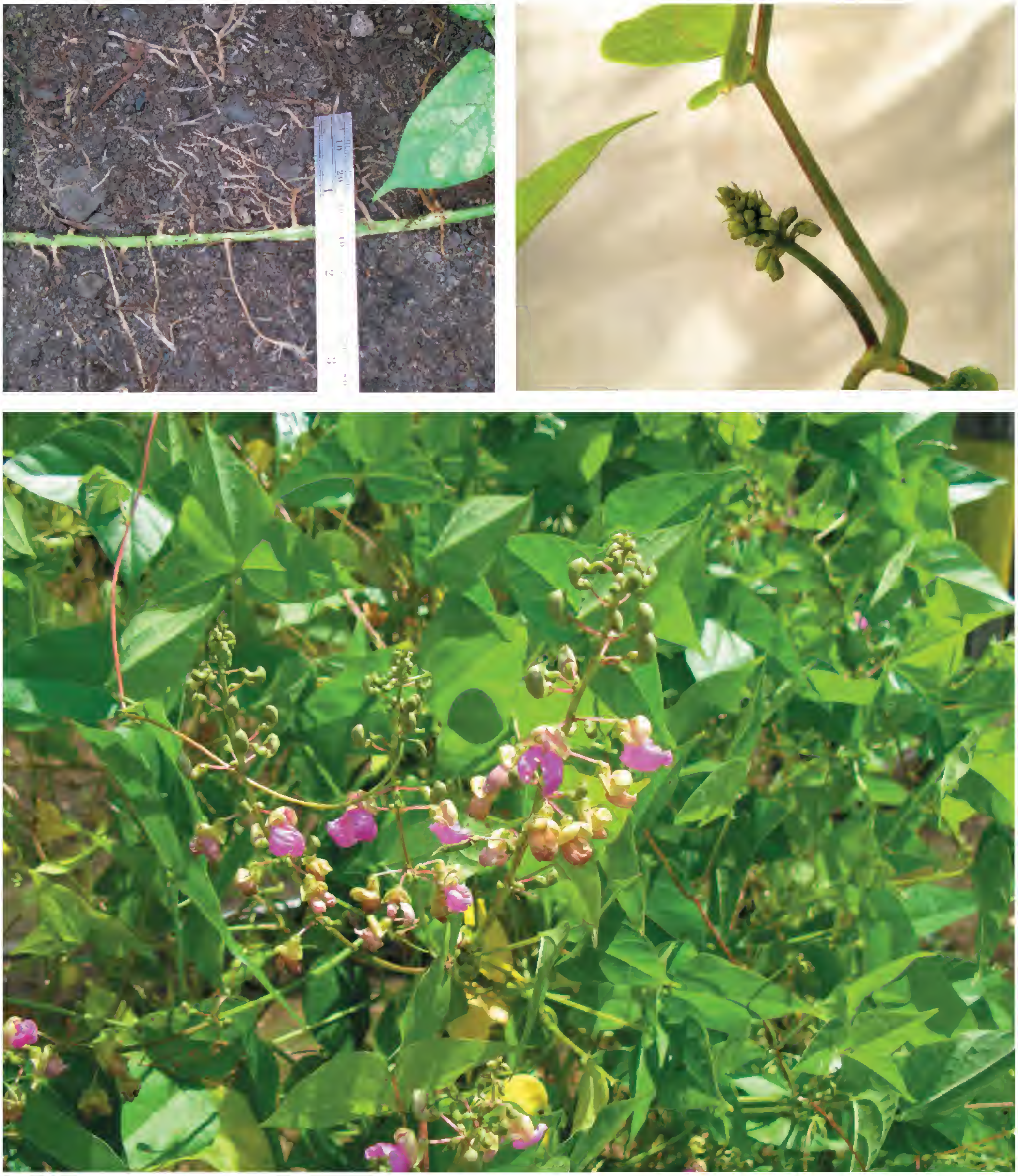

Fig. 2. Photographs of different parts of *P. lignosus*. Top left: rooting lower internode. **Top right:** young developing raceme. **Lower part:** blooming stems.

During growing-out the plant showed a dual growth habit with 2–4 m long guides sprouting from lower nodes of main stem and spreading on the ground, and main stem and other guides from upper nodes continuing climbing upwards. The stems spreading on ground have a significant capacity to quickly produce adventitious roots (Fig. 1f, Fig. 2 top left). One plant in Popayán produced white flowers (see Fig. 5 for comparison); white flowers were also noted at collection site, as indicated on the label of *C Watlington CW3* at K (Debouck 2014), evidencing a good sampling by MSB for seed distribution. The original description by Britton reported white flowers too; unless otherwise indicated the description above refers to the magenta-flowered plant. It is

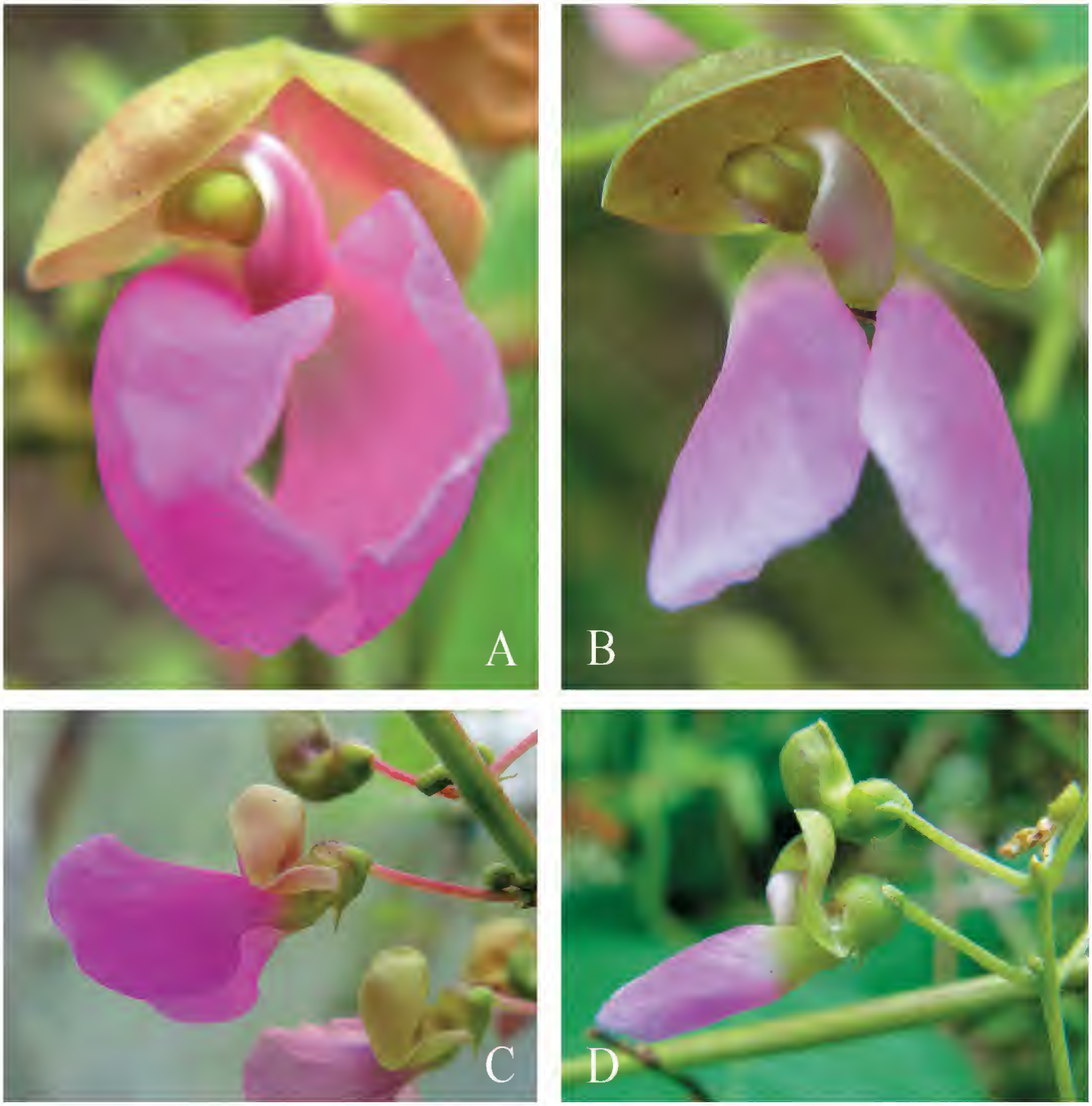

Fig. 3. Close-up of flowers, **top:** front view (a,b), and **below:** lateral view (c,d). **Left side** (a,c): *P. lignosus* (*C Watlington 3; G40876*; epitype). **Right side** (b,d): *P. lunatus*, wild form (*DGD-3236; G27609*).

important to note that the white-flowered variant has the same black speckled seed just as described above for the magenta-flowered variant. The material seems to be susceptible to spider mites and nematodes (*Meloidogyne*). Pulvini are active in sunshine spots with the blades of leaflets turning parallel to solar radiation by midday (Fig. 2 lower part).

Diagnosis and recognition

As indicated in the Discussion below the most relevant taxon with which *P. lignosus* is to be related to and distinguished from is the wild form of *P. lunatus* present in Central America and the Caribbean.

Herba mox perennis cum caulibus inferioribus prostratis dum superioribus volubilibus. *P. lunati* L. affinis sed foliolis ovatis floribus majoribus vexilliique superficie externa glabra, leguminibus majoribus angustioribus. Habitat solum in sylvis propemodo destructis insularum maximarum Bermudae archipelagi rarus.

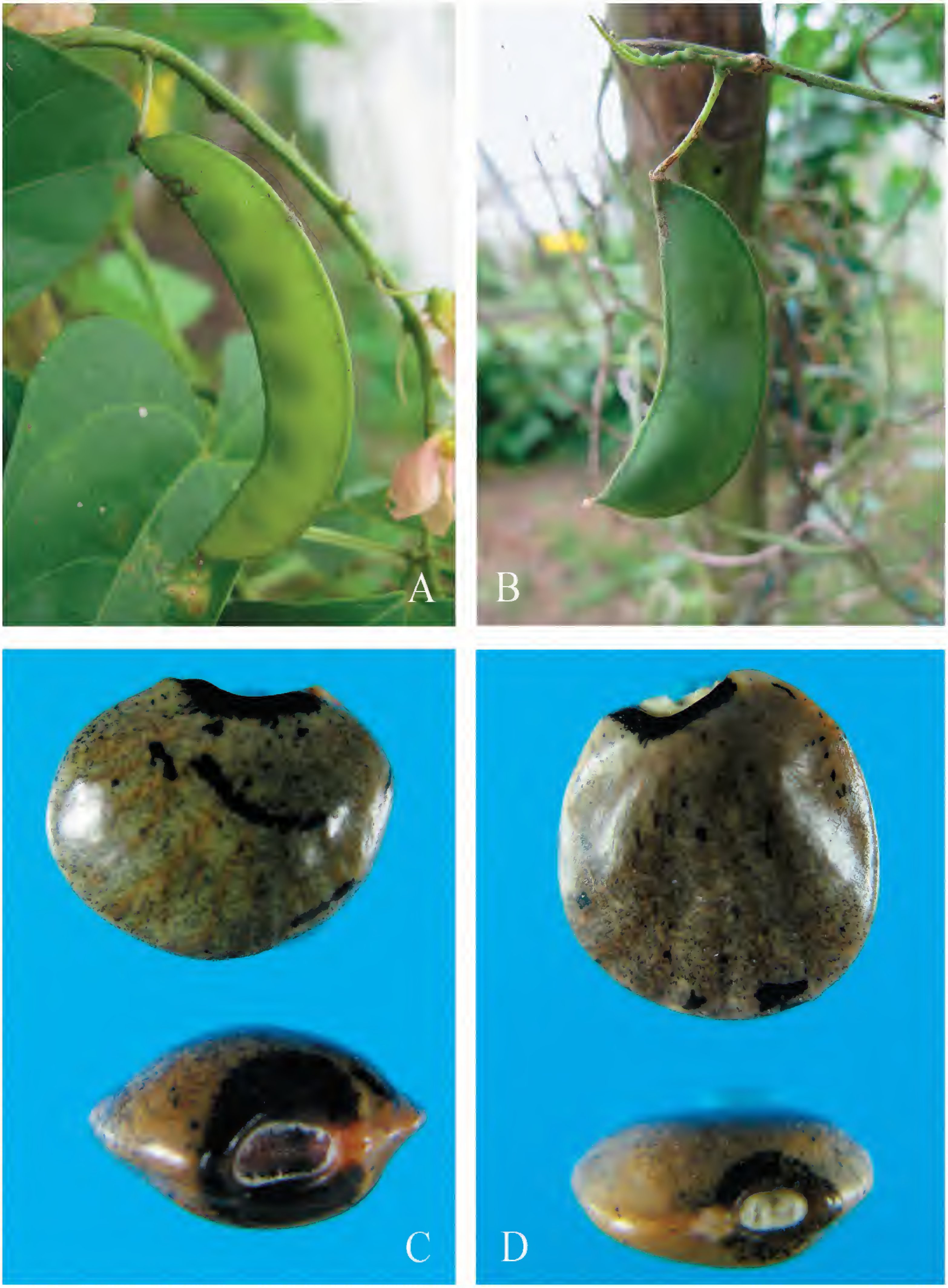

Fig. 4. Close-up of pods (top: a,b) and seeds (below: c,d; scale bar = 1 mm each). **Left side** (a,c): *P. lignosus* (*C Watlington 3; G40876*; epitype). **Right side** (b,d): *P. lunatus*, wild form (*DGD-3236; G27609*).

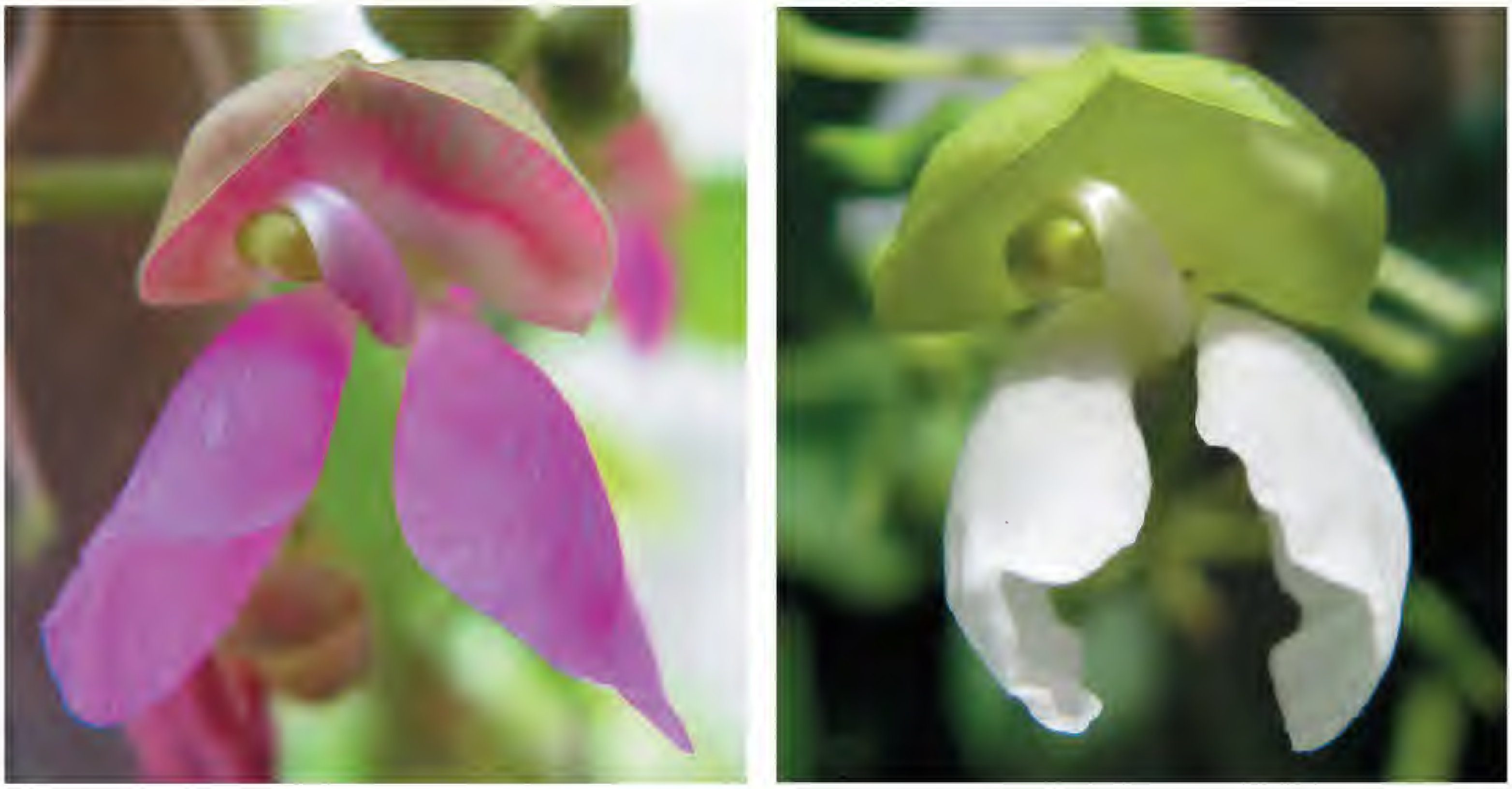

Fig. 5. Close-up front photographs of flowers of *P. lignosus* at anthesis. Left: normal wild type. Right: white flowered variant. Both plants from original collection CW3, increased and conserved as accessions G40876 and G40876A, respectively.

Flower twice as large as the one of wild Lima bean ('Mesoamerican', see Discussion), with glabrous standard and magenta wings (Fig. 3a,c) in contrast to the outer upper pubescent face of standard and lilac wings in the latter (Fig. 3b,d), are some distinctive characteristics of *P. lignosus*. Leaflets in wild Lima bean are usually lanceolate while ovate in the Bermuda bean (lower half of lamina constantly more rounded in the latter as compared to wild *P. lunatus*). The longer and narrower pod (because it usually has one more seed; Fig. 4a) of *P. lignosus* as compared to wild *P. lunatus* (41 mm long, 12 mm wide, 5.5 mm thick; Fig. 4b) is worth mentioning, as are the more rounded seeds and absence of seed ridges radiating from the hilum in the former taxon (Fig. 4c). In CIAT experimental station at Popayán, the time elapsed between anthesis and physiological maturity of pod is forty days or one additional week as compared to wild Lima bean planted in the same conditions.

Additional Specimens

Five specimens (although *Brown 718* and *Brown 1179* might be from the same population visited at different dates) were seen by the author in 75 out of 82 Herbaria keeping Paniculati specimens and visited since 1977 (see list in Acknowledgments below; data as on the labels):

BERMUDA: Joyce Dork [or Dock?] Cave, 22 May–2 Jun 1909, *Stewardson Brown 718* (US); thicket [indication of vegetation?], Joyce's Dock, 29 Nov–14 Dec 1912, *Stewardson Brown 1179, NL Britton, Fred J Seaver, collectors* (US); Hamilton Parish, Idwal Hughes Nature Reserve, along trail east of west sink, Walsingham, 22 Feb 2007, *MA Hamilton 610* (K); Castle Harbour Golf Course [32° 20' 30"N, 64° 43' 30"W; our estimate], 5 May 1964, *E Manuel 637* (A); Bermuda [sic!], Warwick, Cluster Cottage Gardens, 25 Apr 2008, *C Watlington 3 with E Morbey* (K; two sheets).

The specimen *Brown 680* mentioned by Delgado-Salinas et al. (1999, 2006) and López-López et al. (2013), and claimed as deposited at PHILA has not been seen because the search for PHILA in *Index Herbariorum* (2013) did not yield any result, nor did the Specimen Search in Tropicos (2013).

Designation of an epitype

As afore-mentioned in the original description (Britton 1918) there is no reference to any plant type specimen, although Britton could have used any of his collections with Stewardson Brown, whom he acknowledged as one of his collaborator (op. cit., p. xi). This situation should thus be corrected, either by using existing exsiccata (see above, Additional Specimens) or by forming new ones, hopefully numerous and complete. Along the former possibility, the material of *S Brown 1179* registered in the United States National Herbarium (US sheet 3413573), Smithsonian Institution in Washington, is not complete enough for a type: no flowers, and pods harvested excessively late (borne on a single raceme pulled out of the main stem!). One of the collectors of this specimen *S Brown 1179* was Britton himself, and he (because it is the same handwriting as in the frontispiece of the biography by E.D. Merril 1938) annotated the voucher prior to its transfer to US (Debouck 2014). Incidentally, this helped us to validate all fruit characteristics (dimensions, curvature, sutures, beak, base). The specimen *MA Hamilton 610* at K lacks fruits as does one duplicate of the *C Watlington 3* collection (K000650153). The specimens *E Manuel 637* (in A) and *C Watlington 3* (K000650154) lack mature pods and seeds, although they are fairly complete but unique. Finally, the specimen *Stewardson Brown 718* (US1341071) with flowers and young pods, although identified by James A. Lackey as *P. lunatus* (Debouck 2014), could help but again is unique. Incidentally, this last identification stresses further our point: the need for good plant specimens to refer to! Following Art. 8, Art. 9.8 and 9.13 and Recommendation 9C.1 of the Melbourne Code (McNeill et al. 2012), using cuttings of the plant grown in Popayán (from seed of the original collection of C Watlington (CW3), an epitype is designated and fourteen isoepitypes were made and deposited into the Herbaria indicated below. The specimen in Kew consists of two sheets (for space reasons only): marked '1/2' with leaves, racemes, flowers, pods and seeds, and '2/2' with root and seedling. Designating an epitype is the least that can be done (because it is to classify plants not drawings!)—not a neotype as we thought at the beginning of this research and distribution of vouchers—as there is a lectotype (an illustration; Art. 9.2).

Phaseolus lignosus Britton. Type: BERMUDA: plant seen in rocky woodlands between Castle Harbor and Harrington Sound, fig. 205, without citation of specimen, collector, or date (lectotype, here designated: Britton, Fl. Bermuda, Fig. 205 on page 183, 1918). (epitype, here designated: K with bar code K000556376 and K000556377; isoepitypes: BRIT, CAS, COL, F, FHO, FI, G, GH, MEXU, MICH, MO, NCU, NY, P). Voucher specimens of the white flowered variant—so indicated—have been deposited into the Herbaria BRIT, K, MICH, MO and P.

Geographic distribution, ecology and conservation status

Specimens studied so far indicate a distribution restricted to the major island of Bermuda: Long Island (above data, and Debouck 2014), with no sure records for the other two large pieces of land: St. George's Island and Somerset Island. The record for Hungry Bay, Paget Parish on Long Island mentioned by Britton (1918), that we have not seen, might be doubtful because it is anterior to the original publication. Christine Phillips-Watlington (1996) reports the Bermuda bean from three areas of Long Island in the Walsingham Cave district only, while Copeland and co-workers (2014) report it from four places. This vinelike legume is part of the understory of the almost gone Upland Woodland with *Juniperus bermudiana* L., *Sabal bermudana* L.H. Bailey, *Celtis laevigata* Willd., *Cassine laneana* (A.H. Moore) J.W. Ingram and *Zanthoxylum flavum* Vahl. (Small 1913; Britton 1918; Phillips-Watlington 1996; Pettit *et al.* 2012). As the wild *P. lunatus* from the Peninsula of Yucatan (Standley 1930; personal observations in February 1979), the Bermuda bean can thrive in karstic derived soils too (Phillips-Watlington 1996). *P. lignosus* is listed as an endangered very rare endemic under the Protected Species Act 2003 of the Government of Bermuda (Pettit et al. 2012), and as 'critically endangered' by the IUCN (Copeland et al. 2014. It is this situation that incited us to use grown cuttings to make a large series of reference specimens available to many Herbaria, rather than taking more reproductive parts from original plants.

DISCUSSION

The above facts elicit the following points for discussion. The **first** point—stressing further the purpose of this note—relates to the question whether or not the plant described above is *P. lignosus*. We only have the original description and a drawing to refer to (Britton 1918, p. 183, Fig. 205), and no reference specimens. The plant described above is a wild bean plant because of pod dehiscence and seed characteristics. It is thus not any form of *P. coccineus* L. (syn. *P. multiflorus* Willd.), *P. lunatus* L.and *P. vulgaris* L., all three grown as garden crops in the archipelago of Bermuda, according to Britton (1918). The vegetative parts (stems, leaves, glabrousity) of *C Watlington 3* grown in our conditions match with the original description (and with specimens *MA Hamilton 610, E Manuel 637*, and *Stewardson Brown 1179*). The minute uncinate hairs however are not mentioned in the original paper; these will be noted later on (Doutt 1932), and their taxonomic value for *Phaseolus sensu stricto* identification will be realized much later (Baudet 1973; Maréchal et al. 1978). The raceme is a curved pseudoraceme as in Fig. 205, and dimensions for peduncle and rachis fit within the range given by Britton. The calyx and wing of the flower match with the original illustration even though most floral parts are wanting. The pods match with the description (except the part in bracket "[*P. semierectus* of Reade]") and with those of *Stewardson Brown 1179* (seen by Britton), namely the beak, the base and fine sutures. The seed displays a sunken hilum as on the illustration in the work of Britton (1918). From this we can conclude that the collection *C Watlington 3* and its afore-mentioned fourteen isoepitype specimens are a *Phaseolus sensu stricto* species (Maréchal et al. 1978; Lackey 1983), and belong to *P. lignosus*.

Nathaniel Lord Britton (op. cit., p. 183) indicated a (morphological) relationship of his new taxon with *P. polystachyus* (L.) B.S.P., not with *P. coccineus* L. (syn. *P. multiflorus* Willd.), *P. lunatus* L. nor *P. vulgaris* L.. This statement would mean that he has noted the differences between all these taxa. And this brings to the **second** point about the nature of this taxon and its relationships with other *Phaseolus* species. We have to examine first whether or not it belongs to the Paniculati section (Freytag & Debouck 2002). The size of the pluriannual plant, its climbing growth habit from a woody lower stem, the leaf morphology, the pseudoraceme and size and shape of the primary bracts and bracteoles, all point to this section. The capacity of the meristems of secondary racemes to produce flowers beyond flower no. 3 is noteworthy. In addition, two phylogenetic analyses (Delgado-Salinas et al. 1999, 2006) have shown that *P. lignosus* belongs to the '*P. lunatus* group', distinct from the '*P. polystachios* group', while both groups have been included into the Paniculati (Freytag & Debouck 2002). So, *P. lignosus* would be an addition to the Lima bean gene pool, the richest in species in the genus (Porch et al. 2013).

The **third** question might be: is *P. lignosus* a species distinct enough from *P. lunatus* and *P. polystachyus* as to deserve the specific rank? Bearing in mind that the closest mainland is North Carolina of USA (Watson et al. 1970), one could also raise a similar question about the Bermuda bean towards *P. sinuatus* Nuttall ex Torrey & Gray and *P. smilacifolius* Pollard, that are distributed in the southeastern USA (Isely 1990, and Small 1903, respectively). Differently lobed leaflets (small rounded lobes in *P. sinuatus* and large 1 cm long rounded lobes in *P. smilacifolius*) of the latter two taxa clearly exclude an identity with the Bermuda bean. *P. lignosus* could not be a variant of *P. polystachyus* either, because its leaflets are not rounded broadly ovate and delicately acuminate, and its pod beak is longer and pointed. Growth of axes of secondary racemes is often seen in *P. polystachyus*, giving a definite panicle aspect to the inflorescence, while not seen in *P. lignosus*. Another major difference is ecological: *P. polystachyus* could experience frost in a significant part of its US continental range (from New York to Missouri: Debouck 2014; Freytag & Debouck 2002), while *P. lignosus* thrives in almost frost-free habitat (Watson et al. 1970; Phillips-Watlington 1996).

The difference with wild *P. lunatus* is a relevant question—and purposely we alluded to it a couple of times already, because the small-seeded wild form (or 'Mesoamerican', not the Andean one: Serrano-Serrano et al. 2010) has towards the northern part of its range a wide distribution from Islas Revillagigedo in the Pacific Ocean, through Sonora and Tamaulipas in Mexico, and then the Greater and Lesser Antilles (Debouck 2014; Freytag & Debouck 2002). The current floristic works for the Bahamas (Britton & Millspaugh 1920; Correll & Correll 1982; Nickrent et al. 1988) do not clearly conclude about the presence of *P. lunatus* as a wild plant or as "spontaneous after cultivation." Would the Bermuda bean be an expansion of wild or weedy *P. lunatus* into the Bermuda archipelago? Although much alike a wild Lima bean during early vegetative growth, the plant differs from the former by its flower, pod and seed characteristics (Figs. 3, 4). The flower of *P. lignosus* is bigger as compared to the one of wild Lima bean; the wings are cupped and almost getting in contact instead of bending forward spatulate and clasping on each other in the latter (Fig. 3b,d). The magenta color (the 'quinacridone' magenta used by botanical illustrators: Stevens 2007) is unknown in wild *P. lunatus*. The pod is not moon crescent shaped as in wild Lima bean, and the pod beak is wider and longer (Fig. 4a) as compared to that of wild Lima bean (Fig. 4b). The time from anthesis to pod maturity is longer in *P. lignosus* as compared to that of wild *P. lunatus*. On the other hand, Pettit and co-workers (2012) indicated that *P. lignosus* would not thrive in salinity affected areas, while wild *P. lunatus* seems to be salinity tolerant at least in some populations (Bayuelo-Jiménez et al. 2002). For these reasons, the Bermuda bean can be considered as a different and valid species.

A **fourth** point is related to the distribution of this taxon, and it seems that definitely *P. lignosus* is endemic to the Bermuda archipelago. All *Phaseolus sensu stricto* species as wild plants are distributed only in the New World (Lackey 1983; Freytag & Debouck 2002), and thus these are the species the Bermuda bean should be compared to in terms of geographic distribution. It has not been reported from the Carolinas (Radford et al. 1968; Debouck 2014). The floras of the Bahamas (Correl & Correl 1982; Nickrent et al. 1988) do not report it either. *P. lunatus* exists as wild in the Greater Antilles (Cuba: Beyra & Reyes-Artiles 2004; Haiti and the Dominican Republic: Debouck 2014; Puerto Rico: Perkins 1907) and Lesser Antilles (Perkins 1907), and seems to be the only true wild *Phaseolus* species there, although *P. dumosus* Macfady. thrives as a weed in mountainous Jamaica (Macfadyen 1837; Freytag & Debouck 2002). There is a report about the presence of *P. polystachyus* in Puerto Rico (Liogier 1988, p. 194, "in thickets at lower elevations, Rincón"), but no specimens are mentioned, and we have not seen so far any specimen of *P. polystachyus* reported from the Caribbean Islands (Debouck 2014). Delgado-Salinas (1985) did not either report any specimen of *P. polystachyus* from the Caribbean. Finally, in addition to being an endemic plant, the low number of populations reported here (and mentioned by Copeland and co-workers, 2014) is stricking: it might reflect a poor sampling of the Bermuda archipelago (made of 180 islands and islets, although few covered originally by the Upland Woodland), or a naturally or human induced low number of populations. This situation deserves additional field work and frequent updating.

In conclusion, Nathaniel Lord Britton was right in identifying *P. lignosus* as a new bean species endemic to the flora of Bermuda. While some of its populations are nowadays at risk in original habitats (29 individuals, and with population trend being evaluated as decreasing: Copeland et al. 2014), a positive note is an increased capacity to produce *ex situ* seeds of this rare taxon through a cooperative effort of CIAT-MSB (at closing of preparation of this note, 6,768 seeds have been harvested at CIAT, and harvests continue). Thanks to seed availability some questions for future research such as: how, when and from where did *P. lignosus* land in the Bermuda archipelago?, or which useful traits could it bring to bean breeding?, can now be addressed.

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BOOK NOTICE

Jesse Vernon Trail. 2015. **Quiver Trees, Phantom Orchids and Rock Splitters: The Remarkable Survival Strategies of Plants.** (ISBN-13: 978-1-77041-208-8, pbk). ECW Press, 2120 Queen Street East, Suite 200, Toronto, Ontario M4E 1E2, CANADA. (**Orders:** ecwpress.com). $24.95 US/CAN, 300 pp., full color throughout, 130 photos and illus., 5" × 7".

From the publisher: Plants around the world are often exposed to bitter cold, relentless winds, intense heat, drought, fire, pollution, and many other adverse growing conditions. Yet they are still able to survive and often even thrive.

Quiver Trees, Phantom Orchids and Rock Splitters: The Remarkable Survival Strategies of Plants is a handy pocket guide to everything you could ever want to know about the tenacity and resilience of plants. Designed with a beautiful full-color layout and peppered with over 130 eye-catching photographs and illustrations, [the book] showcases the many weird and wonderful ways that plants adapt to survive and spread their progeny. The book offers absorbing information that will inspire a new respect for nature's innovation and resilience.

Jesse Vernon Trail is an author, instructor, and curriculum developer in environment, ecology, sustainability issues, horticulture, and the natural history of plants. He has had articles published in *The Ecologist, Garden Making, Canadian Gardening, Plant and Garden, Fine Gardening, Gardenwise, Harrowsmith Country Life, Alive,* and *Outdoor Canada*. Jesse lives in Vernon, B.C.

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DASYLARYNX ANOMALUS GEN. ET SP. NOV., A TUBULAR MONOCOTYLEDON-LIKE FLOWER IN MID-TERTIARY DOMINICAN AMBER

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ABSTRACT

Dasylarynx anomalus is described as a new genus and species, based on two flowers preserved in Mid-Tertiary amber from the Dominican Republic. The fossil is hypothesized as being adapted for pollination by hummingbirds or long-tongued insects, with a slender perianth tube formed of 3 fused petals. The flower is bisexual, the stamens being positioned at the base of the corolla tube together with a single stipitate pistil. The tube is densely hirsute within, bearing trichomes from base to apex. The trichomes, although appearing stiff, were evidently flexible enough to allow the bills or mouthparts of visiting pollinators to reach the source of food. Only part of the androecium is visible. The fertile stamens are club-shaped, with introrse dehiscence. They are accompanied by several lattice-like staminodes that are perforated by numerous openings of various sizes. The combination of unique androecial characteristics, together with a tubular, non-lobed corolla, makes it difficult to place the fossil in any modern family of monocotyledons.

RESUMEN

Dasylarynx anomalus se describe como un Nuevo género y especie, basados en dos flores conservadas en ámbar del Terciario medio de la República Dominicana. El fósil se supone estar adaptado para la polinización por colibríes o insectos de lengua larga, con un tubo de perianto delgado formado por tres pétalos unidos. La flor es bisexual, los estambres están posicionados en la base del tubo de la corola junto con un pistilo estipitado simple. El tubo es densamente hirsuto en el interior, llevando tricomas de la base al ápice. Los tricomas, aunque parecen rígidos, eran suficientemente flexibles para permitir a los picos o partes bucales de los polinizadores visitantes alcanzar el recurso alimenticio. Solo es visible una parte del androceo. Los estambres tienen forma de porra, con dehiscencia introrsa. Están acompañados de varios estaminodios en forma de rejilla que están perforados por numerosas aberturas de varios tamaños. La combinación características únicas del androceo, junto con una corola tubular, no lobulada, hace difícil situar el fósil en cualquier familia moderna de monocotiledóneas.

INTRODUCTION

The Mid-Tertiary Caribbean forests giving rise to Dominican amber were described by Poinar and Poinar (1999), based on the known insect fauna and a limited number of available plant fossils. Since then, numerous additional examples of the flora have been discovered, in the form of amber-embedded flowers of various forest-dwelling taxa. The plant species producing the resin that trapped these fossils was *Hymenaea protera* (Poinar 1991), a leguminous tree related to present-day *Hymenaea courbaril* L. *Dasylarynx anomalus*, the subject of this paper, is the 20th angiosperm species to be described from Dominican amber. Besides *H. protera*, these include 2 species of Fabaceae (Dilcher et al. 1992, Poinar & Chambers 2015), 2 of Poaceae (Poinar & Judziewicz 2005; Poinar & Columbus 2012), 3 of Arecaceae (Poinar 2002a, 2002b), 1 of Chrysobalanaceae (Poinar et al. 2008a; revised by Chambers & Poinar 2010), 2 of Lauraceae (Chambers et al. 2011a, 2012), 3 of Meliaceae (Chambers et al. 2011b; Chambers & Poinar 2012), 1 of Burseraceae (Chambers & Poinar 2013), 1 of Myristicaceae (Poinar & Steeves 2013), 1 of Rhamnaceae (Chambers & Poinar 2014a), 1 of Ticodendraceae (Chambers & Poinar 2014b), and 1 possibly of Moraceae (Poinar et al. 2008b).

Having 2 specimens of the *Dasylarynx* flower, it was possible to grind and polish the corolla tube of 1 to expose the anthoecium and gynoecium, as well as to reveal the dense inner covering of trichomes. In the process, however, the stamens were disturbed, and some pollen was scattered that partially obscures the manner of anther dehiscence and other structural features. The stipe, ovary, and style of the pistil, partly visible among the trichomes, are indicated in Fig. 2. Nine stamens are assumed to be present, but only 5, including 3 stami-

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nodes, are shown in the polished section (Fig. 3). The total number of fertile stamens is unknown, since only part of the androecium is in view.

The assignment of *Dasylarynx* to the Monocotyledonae is consistent with its monocolpate pollen (Fig. 5) and a perianth formed by 2 whorls of 3 parts, assuming our interpretation of the corolla is correct. Besides the non-lobed corolla tube, other morphological features of the fossil are notable. Taking the place of 3 of the 5 visible stamens are peculiar staminodes, which are thin and lattice-like in construction, variable in shape, and perforated by different sized openings (Fig. 3). The manner of introrse anther dehiscence is not clear but is perhaps by 4 pores (Fig. 3). The pistil is not completely exposed for analysis, but because of the single style and lack of obvious lobing of the ovary, it most likely is composed of a single carpel. Our hypothesis concerning details of the species' pollination syndrome is discussed in a later section of the paper.

MATERIALS AND METHODS

Dominican amber has been assigned to the Mid-Tertiary period, based on planktonic fossils occupying the marine strata in which it is deposited. Mines are located in the Central Mountain Ranges of Hispaniola, from which the amber is extracted by workers who dig lengthy tunnels to reach the sought-after deposits. Samples of amber, brought to the surface, are then sold at the mine entrance or are put on the market for buyers of this semi-precious gemstone. Two differing dates have been proposed for the amber. Iturralde-Vinent & MacPhee (1996) estimated an age of 20–15 Ma, based on foraminifera, whereas 45–30 Ma was the date given by Cépek (in Schlee 1999), derived from studies of coccoliths. The strata containing the amber are turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994).

The flowers are contained in blocks of amber measuring 25 mm × 20 mm × 5 mm (holotype) and 25 mm × 12 mm × 4 mm (paratype). Examination and photographs were made with a Nikon stereoscopic microscope SMA-10-R at 80× and a Nikon Optiphot microscope at 800×.

DESCRIPTION

Dasylarynx Poinar & K.L. Chambers, gen. nov. Type Species: *Dasylarynx anomalus* Poinar & K.L. Chambers, sp. nov. (**Figs. 1–5**).

Diagnosis.—Plants hermaphroditic, flowers stout-pedicelled, perianth biseriate, sepals 3, petaloid, spreading, glabrous, equal or unequal, ovate-lanceolate, with numerous parallel veins from the base, apex obtuse (Fig. 1), petals probably 3, completely fused into an elongate, externally glabrous tube, lobes 0, interior of tube hirsute nearly throughout (Fig. 2), stamens basal in the tube, 9 (?), probably in 3 whorls of 3, including an unknown number of sterile staminodes, 2 fertile stamens visible, club-shaped, with broad, irregularly perforated filaments (Fig. 3F), the anther portion terminal, not much enlarged, introrsely dehiscent, perhaps with 4 pores arranged as 2 pairs, 1 pair above the other (Fig. 3A), staminodes variable in shape, thin, perforated by small or large openings (Fig. 3B, D, E), pistil 1, ovary elliptic-fusiform, glabrous, stipitate, style 1, terminal, elongate, partly obscured by trichomes (Fig. 2), stigma not visible, pollen ellipsoidal, monocolpate (Figs. 4, 5), exine minutely echinate, the spinules in +/- parallel rows, each spinule arising from a small basal cushion (Fig. 4).

Dasylarynx anomalus Poinar & K.L. Chambers, sp. nov. Type: HISPANIOLA. Dominican Republic: amber mine in the northern mountain ranges (Cordillera Septentrional), 1986, *unknown amber miner s.n.* (holotype: catalog number Sd-9-60A; paratype: catalog number Sd-9-60B, both deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.

Description.—Total length 15.6 mm (holotype), largest sepal of outer whorl 9.8 mm long, 4.1 mm wide, other 2 sepals shorter (lengths 7 mm and 6 mm), perhaps due to shrinkage during preservation in the resin (Fig. 1), tube formed by petals of inner whorl 15 mm long, the opening 1.3 mm wide, diameter 2.5 mm below apex, 1.8 mm in center, 1.9 mm at base (Fig. 1), ca. 9-veined near base, hirsute trichomes within tube up to 1.0 mm long (Fig. 2), fertile stamens 1.0 mm long, 0.33 mm wide (Fig. 3), staminodes 0.6–1.1 mm long, up to 0.22 mm wide (Fig. 3), style slender, elongate, ovary 0.73 mm long, 0.36 mm wide, stipe 0.75 mm long (Fig. 2), dimensions of pollen 86 µm × 65 µm (Fig. 4).

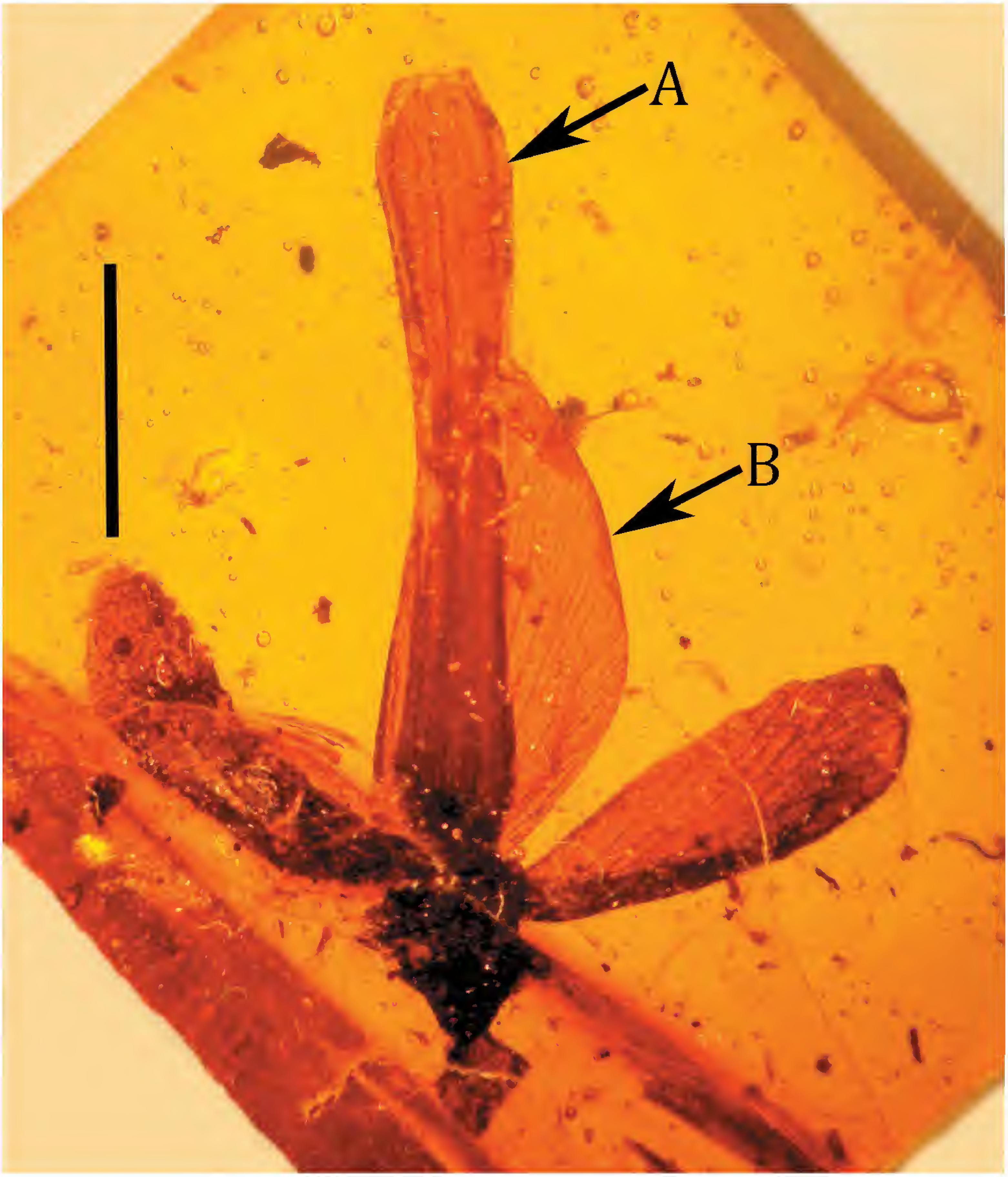

Fig. 1. ***Dasylarynx anomalus*****. Holotype flower, lateral view. A. Corolla tube. B. Sepal. Scale bar = 5.0 mm.**

Etymology.—Genus name from Greek "dasys," hairy, shaggy, and "larynx," throat, gullet. Species name from Greek "anomalos," unusual, abnormal.

DISCUSSION

The floral morphology of *Dasylarynx* is so unusual that its placement in a modern family is problematic. We believe that an androecium of 3 whorls can be identified, consisting of a mixture of fertile stamens and variably perforated staminodes. Anther dehiscence by 4 pores in 2 superposed pairs is hypothesized (Fig. 3). Three

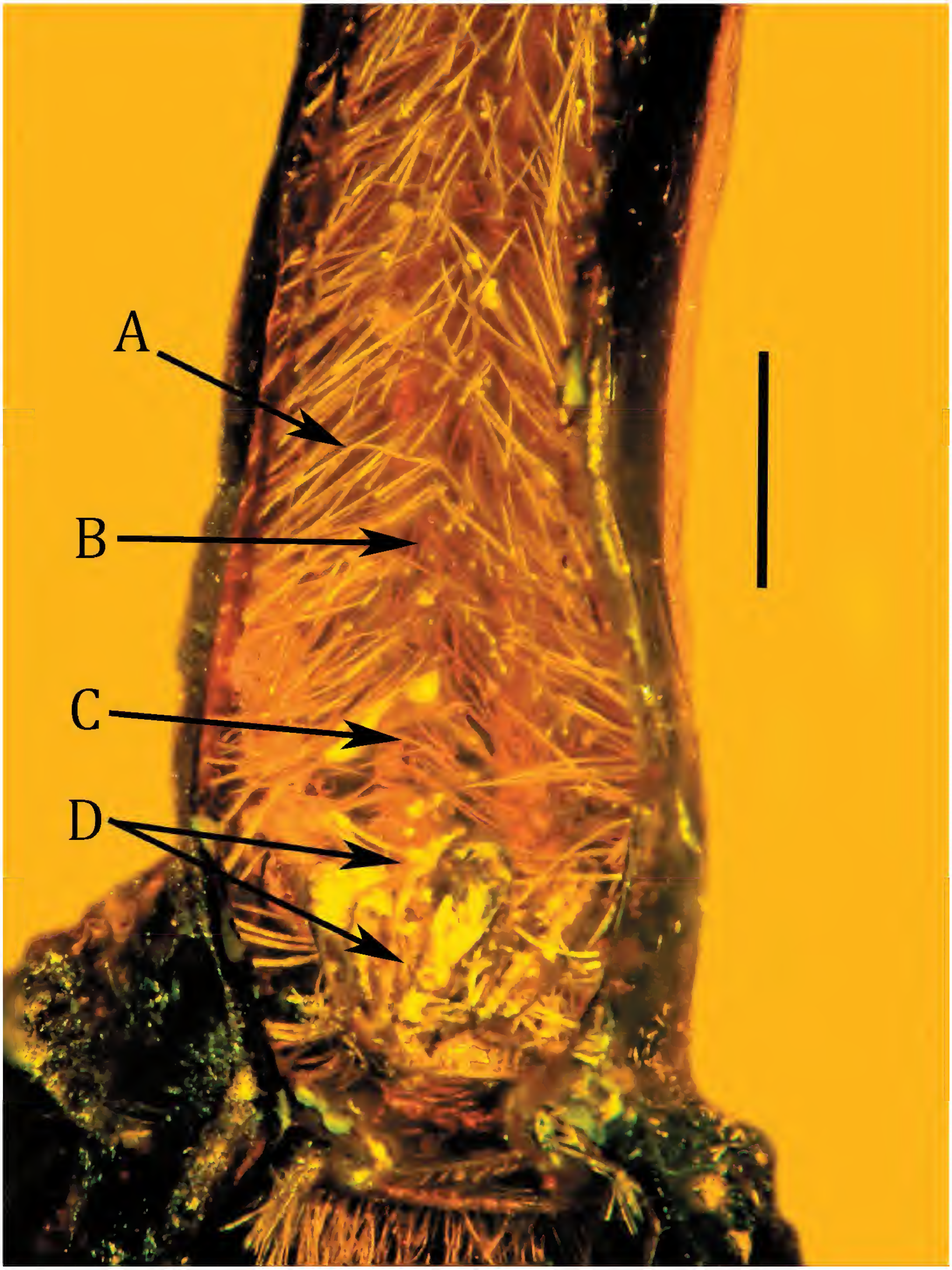

Fig. 2. *Dasylarynx anomalus*. Paratype flower, inside of perianth tube. **A.** Hirsute trichomes. **B.** Style. **C.** Ovary. **D.** Stipe. Scale bar = 1.0 mm.

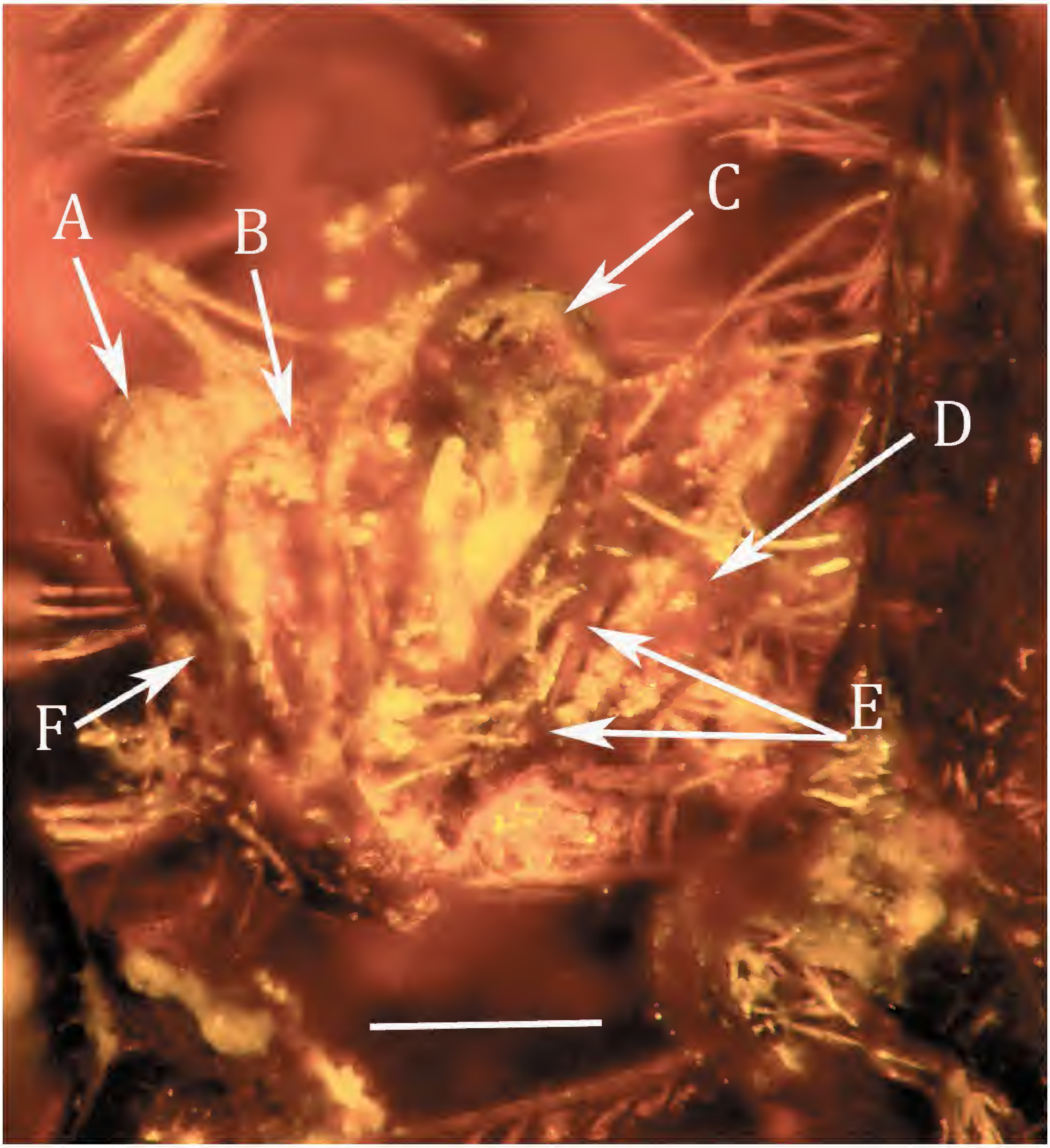

Fig. 3. ***Dasylarynx anomalus*****. Paratype flower, enlarged view. A.** Fertile stamen **B.** Staminode of outer androecial whorl. **C.** Fertile stamen of 2nd whorl. **D.** Staminode of outer whorl. **E.** Staminode of 3rd whorl, interior to fertile stamen. **F.** Perforation in filament of fertile stamen. Scale bar = 0.2 mm.

visible staminodes are constructed of thin, lattice-like strands of differing sizes and are perforated by a variable number of large and small openings. The function of such organs can hardly be guessed at. No nectar glands are present, although a floral disc interior to the stamens may be present. Pollen grains were observed to be monocolpate (Fig. 5), with the exine echinate and the spicules borne on basal cushions (Fig. 4). This type of spicule was observed and illustrated independently in pollen of the Lauraceae (Raj & van der Werff 1988). It is a question whether the 3 sepals were equal or of different sizes. Because the tissue of the left and right sepals (Fig. 1) appears to have shrunken somewhat during preservation, we favor the interpretation that they were of equal size in life.

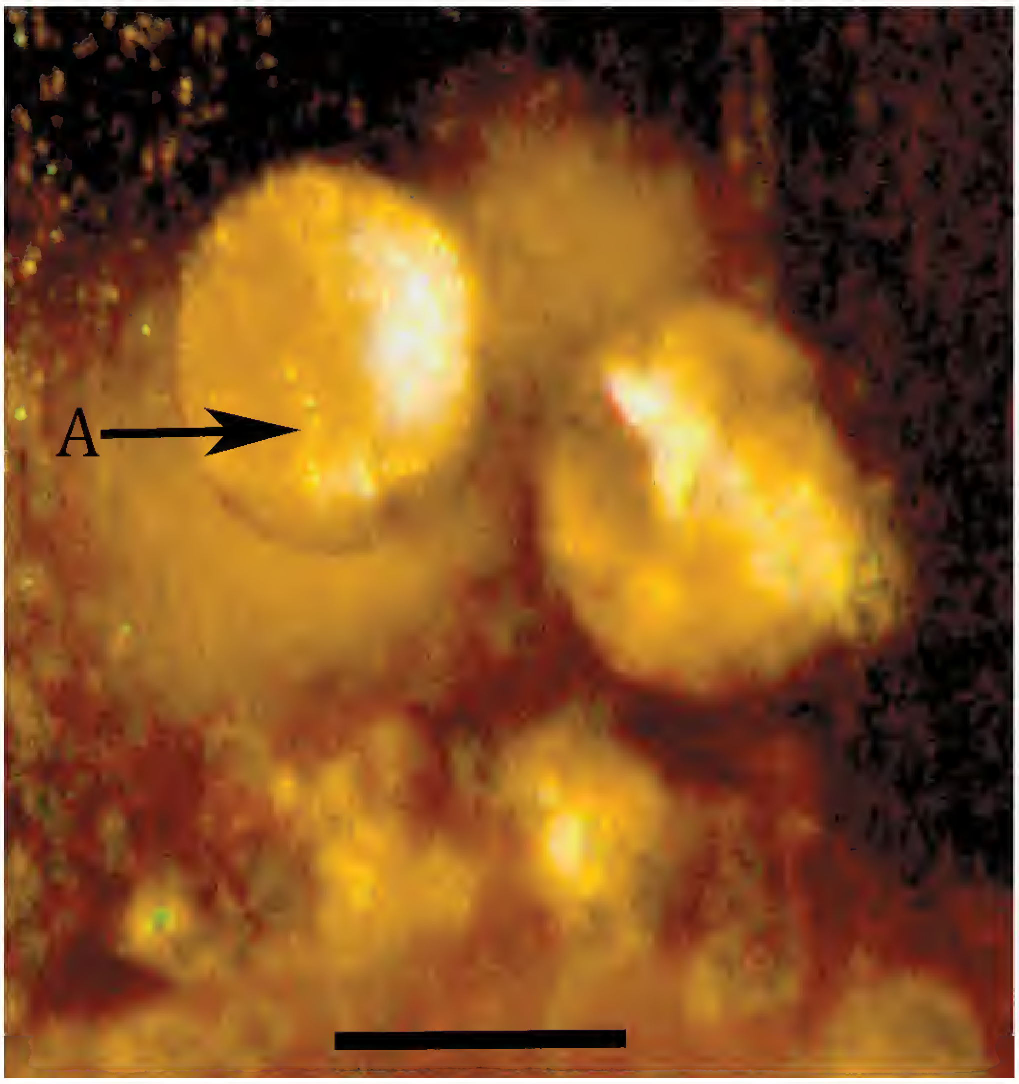

Fig. 4. ***Dasylarynx anomalus*.** **Pollen grain. Arrow shows row of spicules, each with a small basal cushion. Scale bar = 65 µm.**

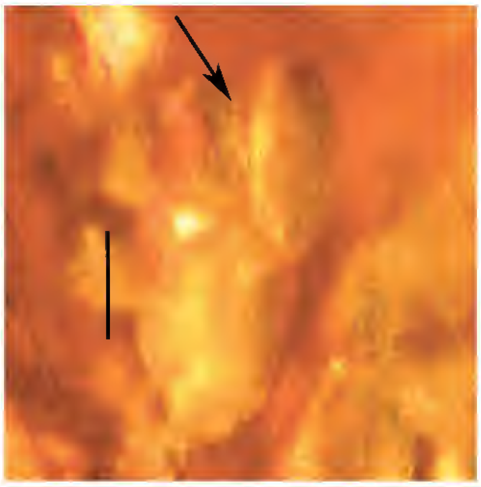

Fig. 5. ***Dasylarynx anomalus*.** **Pollen grain, with arrow on colpus. Scale bar = 46 µm.**

In considering the reproductive syndrome of this flower, we propose that, in spite of its relatively small size, it may have been attractive to hummingbirds, especially if a nectar disc was present at the base of the pistil. In addition, it could have been visited by long-tongued insects, including species of large-bodied bees, flies, or lepidoptera, particularly sphingid moths. Some of the insect groups mentioned by Renner and Feil (1993, Table 1) as pollinators of tubular topical flowers are known to have been present in the Dominican Tertiary forest. These include riodinid and nymphalid butterflies (De Vries & Poinar 1997; Hammond & Poinar 1998), tabanid horseflies (Lane et al. 1988), and euglossine bees (Poinar 1998). Pollinators attracted by the petaloid sepals would have inserted their bills or mouth parts into the perianth tube in search of nectar or pollen. Attached pollen would then be transferred to the stigma of the same or a different flower. Of further note is the hirsute inner epidermis of the floral tube. How this might have played a role in pollination is not clear, but at least it should not have prevented extraction of pollen by the pollinator's bill or tongue. Possibly the corolla hairs functioned to protect against the theft of nectar by small ants.

Bird and insect pollination is common in modern tropical forest woody plants (Bawa et al. 1985). Stiles (1978, Appendix 1) provides a useful list of plant genera that he observed being pollinated by hermit and non-hermit hummingbirds in Finca La Selva, Costa Rica. Among these is *Calathea*, of the Marantaceae. Similarities between the fossil and this family are the presence of a corolla tube, which in Marantaceae is a 3-lobed floral tube including androecium (Andersson 1998), and of 2–4 staminodia in the androecium. These organs are petaloid and hooded or indurate in Marantaceae (Andersson op. cit.), unlike those of *Dasylarynx*. Important differences are that the ovary of Marantaceae is inferior, there is 1 petaloid stamen with a single theca, and the pollen is nonaperturate (Erdtman 1952).

It was noted in the Introduction that this newly recognized genus is one of some 20 taxa that have recently been described from Dominican amber. The environment in which these species grew was considered by Hammel and coauthors (Hammel & Zamora 1990; Hammel & Burger 1991) to have been part of a once widespread Laurasian warm climate forest flora of the Tertiary Period. This mild, humid, aseasonal climate was prevalent across the Northern Hemisphere in Paleogene times (65–25 Ma). Dominican amber, though of uncertain age, can probably be dated to the late Oligocene or early Miocene.

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PRIORIA DOMINICANA SP. NOV. (FABACEAE: CAESALPINIOIDEAE), A FOSSIL FLOWER IN MID-TERTIARY DOMINICAN AMBER

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ABSTRACT

Prioria dominicana is a newly described species of Fabaceae from the Mid-Tertiary tropical forests of the Caribbean island of Hispaniola. These forests were earlier described by Poinar and Poinar (1999) based on the flora and fauna preserved in amber from the fossilized resin of *Hymenaea protera* (Poinar 1991). The single living neotropical species of *Prioria, P. copaifera*, is found in Jamaica, Nicaragua, Panama, and Colombia. It differs from *P. dominicana* in the greater size of its bracts, absence of a pedicel, conspicuous anther connectives, and the villous pubescence of its filaments and ovary. In comparing the fossil with Old World species of *Prioria*, *P. dominicana* shares important similarities with the West African species *P. mannii* and *P. joveri*. It provides evidence, therefore, for a long-standing phylogenetic connection between the Old and New World elements of the genus dating to the Middle or Early Tertiary. Lacking fruits or leaves, further comparison of *P. dominicana* with its relatives is not possible at present.

RESUMEN

Prioria dominicana es una nueva especie descrita de Fabaceae de los bosques tropicales del Terciario medio de la isla caribeña la Hispaniola. Estos bosques fueron descritos previamente por Poinar and Poinar (1999) basados en la flora y fauna conservada en ámbar de la resina fosilizada de *Hymenaea protera* (Poinar 1991). La única especie neotropical viviente de *Prioria*, *P. copaifera*, se encuentra en Jamaica, Nicaragua, Panamá, y Colombia. Se diferencia de *P. dominicana* en el mayor tamaño de sus brácteas, ausencia de pedicelo, conectivos de las anteras manifiestos, y la pubescencia villosa de sus filamentos y ovario. Comparando el fósil con especies del Viejo Mundo de *Prioria*, *P. dominicana* comparte importantes similitudes con las especies del oeste africano *P. mannii* y *P. joveri*. Esto es la prueba, por tanto, de una conexión filogenética de larga duración entre elementos del Viejo y del Nuevo Mundo del género desde el Terciario medio o temprano. Con la falta de frutos u hojas, comparaciones posteriores de *P. dominicana* con sus parientes no es posible actualmente.

INTRODUCTION

The Mid-Tertiary moist, tropical forests of the Caribbean region have come to be better known floristically from studies of fossil amber flowers from the Dominican Republic. Genera from the following families of angiosperms have been described from the amber: Fabaceae (Poinar 1991, Dilcher et al. 1992), Arecaceae (Poinar 2002a, 2002b), Poaceae (Poinar & Judziewicz 2005, Poinar & Columbus 2012), Chrysobalanaceae (Poinar et al. 2008a, corrected by Chambers & Poinar 2010), Lauraceae (Chambers et al. 2011a, 2012a), Meliaceae (Chambers et al. 2011b; Chambers & Poinar 2012a, 2012b), Burseraceae (Chambers & Poinar 2013), Myristicaceae (Poinar & Steeves 2013), Rhamnaceae (Chambers & Poinar 2014a), Ticodendraceae (Chambers & Poinar 2014b), a possible Moraceae (Poinar et al. 2008b), and an unknown monocotyledon (Poinar & Chambers 2015).

The type species of *Prioria*, *P. copaifera* Griseb., is a resin-producing tree up to 40 m high found in low- to medium-elevation forests of Nicaragua, Panama, Colombia, and Jamaica (Woodson & Schery 1951). The genus was long assumed to be endemic to the New World. However, Breteler (1999) proposed an alternative circumscription that expands *Prioria* to include the Old World *Kingiodendron* Harms 1897, *Oxystigma* Harms 1897, *Pterygopodium* Harms 1913, and *Gossweilerodendron* Harms 1925. *Prioria* is classified in the Caesalpinioid tribe Detarieae (Lewis et al. 2005), the largest tribe in the subfamily, with around 84 genera (Fougère-Danezan et al. 2010). In some previous studies, *Prioria copaifera* and its Old World relatives form a clade separate from, but sister to, Detarieae sensu lato (Bruneau et al. 2001; Wojciechowski et al. 2004; Lavin et al. 2005).

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The later work of Bruneau et al. (2008) places the *Prioria* clade as sister to the Deterieae sensu stricto, thus supporting the resin-producing Deterieae clade as monophyletic. The dating of this clade will be discussed in a later section.

MATERIALS AND METHODS

Dating of Dominican amber is still controversial, with the youngest proposed age of 20–15 Ma based on foraminifera (Iturralde-Vinent & MacPhee 1996) and the oldest of 45–30 Ma based on coccoliths (Cépek in Schlee 1990). Most of the amber is secondarily deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994). Dilcher et al. (1992) suggested that "...the amber clasts, from all physical characteristics, were already matured amber at the time of re-deposition into marine basins. Therefore, the age of the amber is greater than Miocene and quite likely is as early as late Eocene." The issue is further complicated by the discovery of Early Oligocene amber in Puerto Rico and Maastrichtian-Paleocene amber in Jamaica (Iturralde-Vinent 2001), indicating that the age of Caribbean amber is still unresolved.

The flower is contained in a block of amber measuring 10 mm × 8 mm × 5 mm. Examination and photographs were made with a Nikon stereoscopic microscope SMA-10-R at 80× and a Nikon Optiphot microscope at 800×. Helicon Focus Pro X64 was used to stack photos for better clarity and depth of field.

DESCRIPTION

Prioria dominicana Poinar & K.L. Chambers, sp. nov. (**Figs. 1–3**). Type: HISPANIOLA. Dominican Republic: amber mine in the northern mountain range (Cordillera Septentrional), 2013, *unknown amber miner s.n.* (holotype: catalogue number Sd-9-23, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower perfect, radially symmetrical, with well-developed pedicel, width at anthesis 3.8 mm (Fig. 1), basally bracteate, bracts 2, separate, elliptic, length 0.6–0.7 mm, width 0.35–0.4 mm, glabrous (Figs. 2, 3), disc apparently 0, calyx 5-merous, sepals free, boat-shaped, broadly ovate, 2.0–2.4 mm long, 1.5–1.9 mm wide, acute, lightly ciliate near tip, otherwise glabrous, midnerve indistinct (Figs. 1, 3), petals 0, stamens 10, free, filaments linear, 3.0 mm long, attached around base of ovary, glabrous throughout (Fig. 2), anthers dorsifixed, ellipsoid, 0.7 mm long, 4-loculed, with narrow connective (Figs. 1, 2), pistil 1, stipe short, glabrous (Fig. 2), ovary ovoid, 1.5 mm long, 1.1 mm wide, glabrous (Fig. 2), style linear, 1.7 mm long, stigmatic tip scarcely enlarged (Figs. 1, 2), floral pedicel 1.1 mm, densely puberulent (Figs. 1, 3).

Etymology.—Species epithet from the Dominican Republic.

DISCUSSION

Prioria dominicana differs from *P. copaifera* in the presence of a puberulent pedicel together with smaller, free, subtending bracts, which in the modern species are orbicular, up to 1.5 mm long, and sheath the disciferous part of the calyx (Woodson & Schery 1951, pers. observ.). The sepals of *P. dominicana* are apparently free and imbricate at the base (Fig. 1) and are not at all scarious margined, as is described for *P. copaifera*. The fossil also differs in the absence of villous pubescence on the filaments and ovary (Fig. 4) and in the less conspicuous connective of the anthers.

The taxonomy of *Prioria* accepted in this paper is that of Breteler (1999, see above). In its similarities to both the Old and New World species of the genus, *P. dominicana* apparently forms a link that helps to unify the genus. Its closest living African relatives, deduced from Breteler's key, descriptions, and illustrations (op. cit.), are *P. mannii* (Baillon) Breteler and *P. joveri* (Aubrév.) Breteler, both native to Cameroun, Guinea, and Gabon. The Indomalasian species of the genus can be excluded from consideration due to their unisexual flowers and crateriform stigmas. *Prioria mannii* has dorsally pubescent sepals, with stamen filaments lightly puberulent at the base, and ovary, together with style base, densely pubescent. Its pedicel is well-developed and puberulent, and its anther connectives are inconspicuous. *Prioria joveri* has dorsally papillate sepals (per Breteler, Fig. 2[2]), puberulent stamen filaments, densely pubescent ovary and style base, and well-developed anther connectives. Its pedicel is densely puberulent. *Prioria dominicana* is similar to both African taxa, therefore, in its

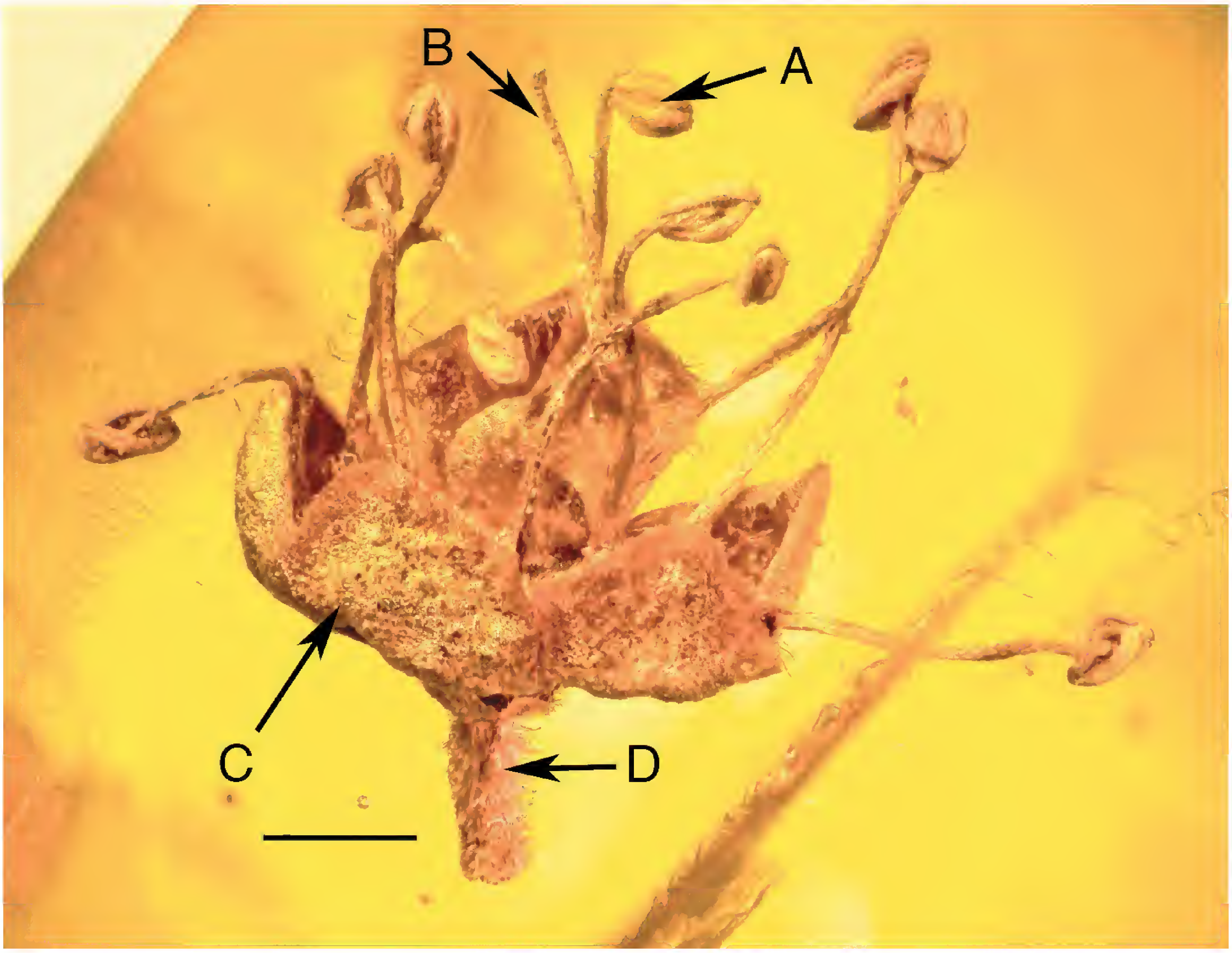

Fig. 1. ***Prioria dominicana*. A.** anther. **B.** style. **C.** sepal. **D.** pedicel.

well-developed, pubescent pedicel (Figs. 1D, 3C) and small bracts, but differs in its glabrous sepals, pistil, and style base.

Discovery a flower in Dominican amber that closely resembles certain African species was previously noted with the fossil *Hymenaea protera*, which has flowers most similar to *H. verrucosa* Gaertn., an extant species restricted to East Africa and adjacent islands (Poinar 1991). In view of the ambiguous age determinations for Dominican amber (see Materials and Methods, above), the timing of its included fossils cannot be clearly assigned at present. One can only speculate on how *Prioria* and *Hymenaea* were able to disperse from Africa to the Caribbean or vice versa. Africa and South America were already separated by the developing South Atlantic Ocean by 94 Ma (http://www.scotese.com/earth.htm); hence, a considerable water gap existed by the time these genera evolved in the Early Tertiary. Various methods of fruit and seed dispersal might be hypothesized that could have allowed elements of the New World tropical forests to overcome this barrier.

In studies pertinent to *Prioria dominicana*, the molecular phylogeny of the Fabaceae has been examined using the chloroplast *trnL* intron (Bruneau et al. 2001), *rbcL* (Kajita et al. 2001), *matK* genes (Wojciechowski et al. 2004), *trnL* intron and *trnL-F* spacer (Fougère-Danezan et al. 2007), and *matK-trnK* plus *trnL* genes (Bruneau et al. 2008). The correlation between molecular and morphological data was examined by Fougère-Danezan et al. (2010). Relationships among the first branching lineages of the legumes are not well supported molecularly, with Cercideae, Detarieae, and the genus *Duparquetia* alternatively resolved as sister group to all of the legumes (Bruneau et al. 2008). In this paper, the authors used 18 well-documented fossils as calibration points, fixing the stem node of the legumes at 65 Ma. Among the fossils included was *Prioria dominicana*,

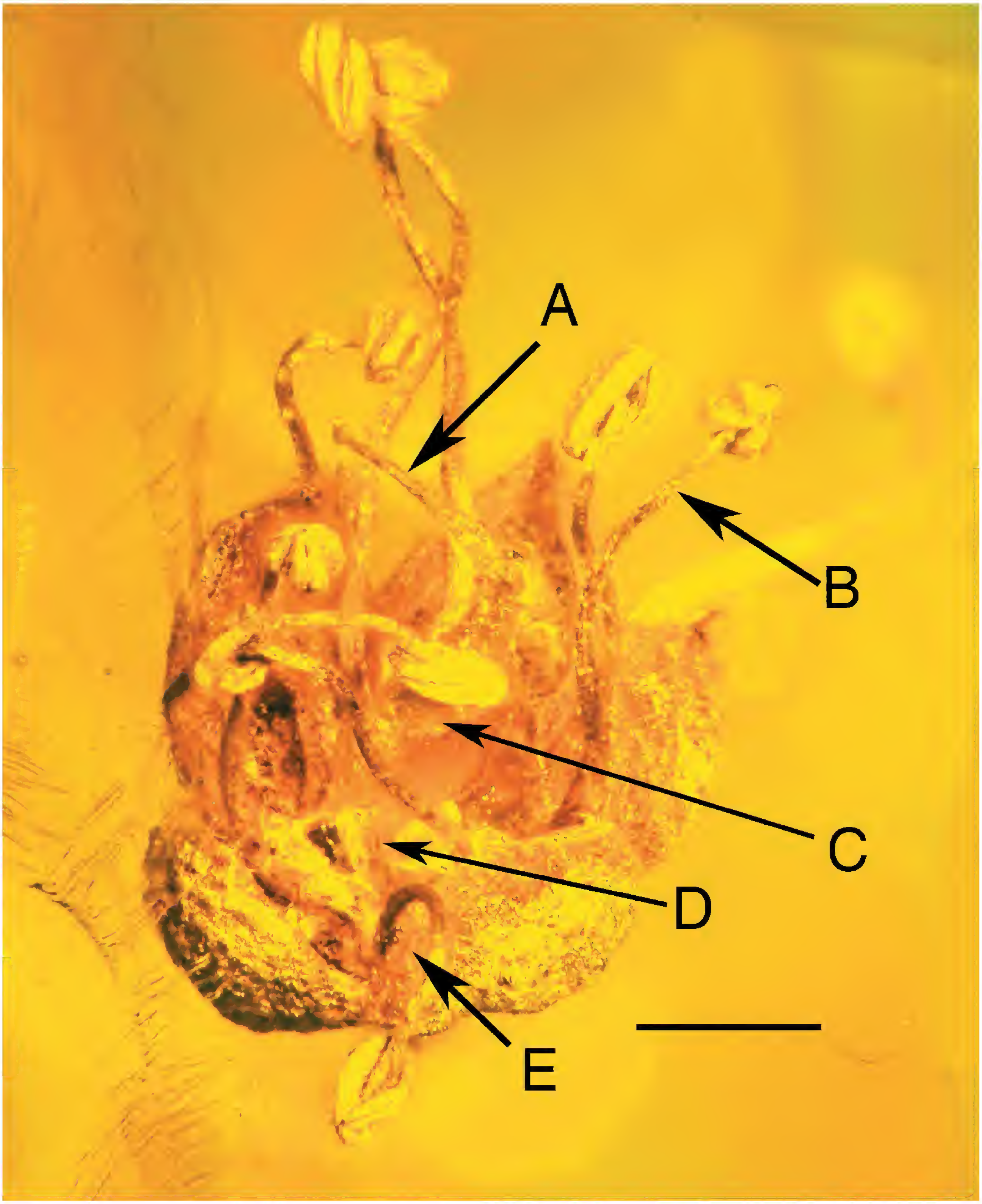

Fig. 2. *Prioria dominicana*. **A.** style. **B.** filament. **C.** ovary. **D.** stipe. **E.** bract.

which prior to its formal description had been illustrated in a book on the Tertiary amber forests of Hispaniola by Poinar and Poinar (1999). As in other studies, Bruneau et al. (op. cit.) could readily define a monophyletic *Prioria* clade, which by their results is sister to the resin-producing Detarieae sensu stricto. Within this clade, *Prioria*, in the broad sense considered here, is assigned a divergence time of ca. 38 Ma (Bruneau et al. op. cit.,

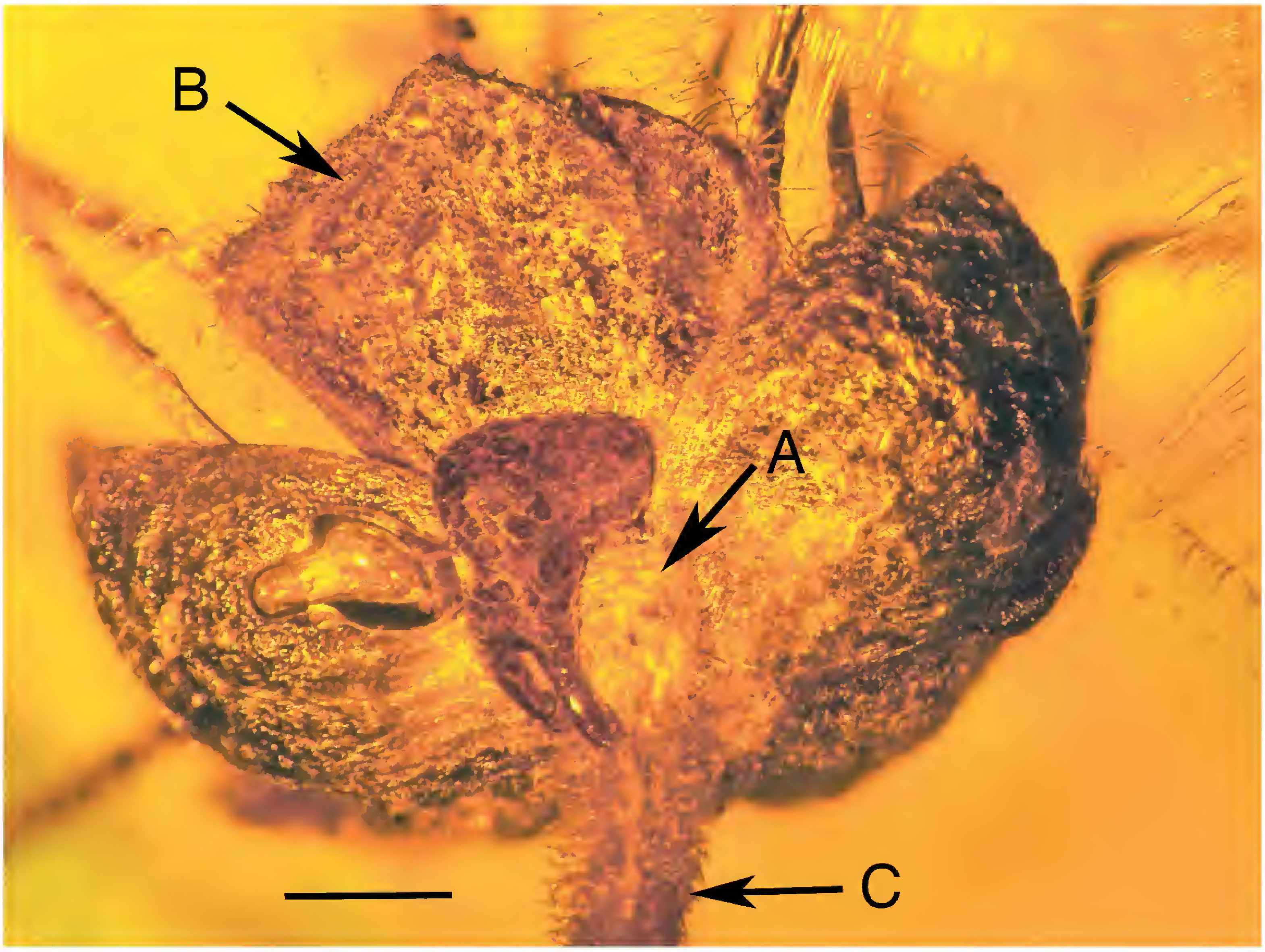

Fig. 3. *Prioria dominicana*. **A.** bract. **B.** sepal. **C.** pedicel. A dark air bubble lies behind the bract.

Fig. 5). As mentioned above, present uncertainty as to the age of Dominican amber fossils implies that more accurate dating to come, if this proves possible, will influence future studies of the age of major Detarieae clades in the Caesalpinioideae.

ACKNOWLEDGMENTS

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ADDENDUM: A GASTEROID FUNGUS, *PALAEOGASTER MICROMORPHA* GEN. & SP. NOV. (BOLETALES) IN CRETACEOUS MYANMAR AMBER

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In the original publication of "A gasteroid fungus, *Palaeogaster micromorpha* gen. & sp. nov. (Boletales) in Cretaceous Myanmar amber" that appeared in J. Bot. Res. Inst. Texas 8(1):139–143 (2014), the MycoBank number of the genus was incorrect. The correct MycoBank numbers are:

Palaeogaster Poinar, Alfredo, & Baseia, gen. nov. (Figs. 1–8), MycoBank no.: **MB 801126.**

Palaeogaster micromorpha Poinar, Alfredo, & Baseia, sp. nov. (Figs. 1–8), MycoBank no.: **MB 801127.**

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BOOK NOTICE

Troy Mcmullin & Frances Anderson. 2014. **Common Lichens of Northeastern North America.** (ISBN-13: 978-0-89327-511-2, hard cover, spiralbound). The New York Botanical Garden Press, 2900 Southern Boulevard, Bronx, New York 10458-5126, U.S.A. (**Orders:** nybgpress@nybg.org, 1-718-817-8721). $39.00 US, 192 pp., 138 color photos, 138 b/w illus., 6 ½" × 9".

From the publisher: At last, a light and easy-to-use field guide to the rich lichen flora of Northeastern North America. The authors have designed this user-friendly guide for amateur naturalists, nature interpreters, forestry workers, land surveyors, researchers, and the general public. Meant to fit in a pocket or backpack, it requires no previous botanical experience and is written in non-technical language.

The 138 lichens in this guide are seen mostly in the Canadian Atlantic provinces, New England, Québec, and eastern Ontario. The guide is formatted so that each page is arranged by the surface each lichen grows on in the field, its shape or growth form, then by its color. Full color photographs and black and white drawings for each species also aid in identification.

Troy McMullin, Ph.D., is a lichenologist and forest ecologist at the University of Guelph. His ecological interests are diverse, but they became focused when he began studying lichens in the old-growth forests of southwestern Nova Scotia as part of his Master's research at Dalhousie University in Halifax. This research led to consulting work on lichens in the public and private sector. He has worked closely with provincial and federal governments in Nova Scotia, Prince Edward Island, and several other Canadian provinces. He completed his doctoral work at the University of Guelph, where he studied the effects of forestry on lichen diversity in northern Ontario.

Frances Anderson, a Research Associate at the Nova Scotia Museum, has published a provisional checklist of larger lichens for Nova Scotia and coauthored research reports into the risk status of two lichen species for the Committee on the Status of Endangered Wildlife in Canada, among other scientific publications. She has done lichen surveys for forestry companies and conservation groups, produced several lichen brochures related to particular geographic areas or hiking trails, written a book chapter on lichens, and led lichen walks for naturalists.

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FURROWED BLISTER PODS STRANDED ON NORTHERN ATLANTIC OCEAN COASTS REPRESENT AN UNDESCRIBED *SACOGLOTTIS* (HUMIRIACEAE) ENDOCARP MOST SIMILAR TO THE FOSSIL *SACOGLOTTIS COSTATA*

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ABSTRACT

Ten distinctly furrowed endocarps stranded on coasts along the northern Atlantic Ocean (including Gulf of Mexico and North Sea) have so far eluded identification. The endocarps resemble the blister pod, a common "sea-bean" originating from the fruit of *Sacoglottis amazonica* (Humiriaceae), but they are larger and show deep furrows. The furrowed blister pods should be classified in the genus *Sacoglottis* sensu lato (*Sacoglottis* and *Schistostemon* together). They represent an undescribed endocarp most similar to the fossil *Sacoglottis costata* Reid from the Tertiary of Colombia, South America. The recent specimens are best denoted as *Sacoglottis* cf. *costata*. Presumably, they do not belong to one of a few *Sacoglottis* species known only from flowering collections. Therefore, it is expected that an undescribed species, producing *costata*-like endocarps, occurs somewhere in northeastern South America.

RESUMEN

Diez endocarpos claramente surcados de las costas del norte del océano Atlántico (incluyendo el Golfo de México y Mar del Norte) habían eludido su identificación. Los endocarpos semejan a una vaina con ampollas, una "sea-bean" común originada del fruto de *Sacoglottis amazonica* (Humiriaceae), pero son más grandes y muestran surcos profundos. Las vainas sulcadas suelen clasificarse en el género *Sacoglottis* sensu lato (*Sacoglottis* y *Schistostemon* juntos). Representan un endocarpo no descrito muy similar al del fósil *Sacoglottis costata* Reid del Terciario de Colombia, Sudamérica. Los recientes especímenes están mejor denominados como *Sacoglottis* cf. *costata*. Presumiblemente, no pertenecen a una o unas pocas especies de *Sacoglottis* conocidas solo de colecciones de flores. Sin embargo, se espera que una especie no descrita, que produce endocarpos semejantes a los de *S. costata*, se de en alguna parte de noreste de Sudamérica.

INTRODUCTION

Sea-beans are "seeds and fruits that are carried to the ocean, often by freshwater streams and rivers, then drift with the ocean currents and (hopefully!) wash ashore" (www.seabean.com 2014). About 2007, a conspicuously furrowed sea-bean (Fig. 1A–D) was found among debris from the North Sea coast in the Netherlands, and brought to the attention of the first author at the end of 2012. This sea-bean closely matched a drawing in the *World Guide to Tropical Drift Seeds and Fruits* (Gunn & Dennis 1976, Fig. 71B;

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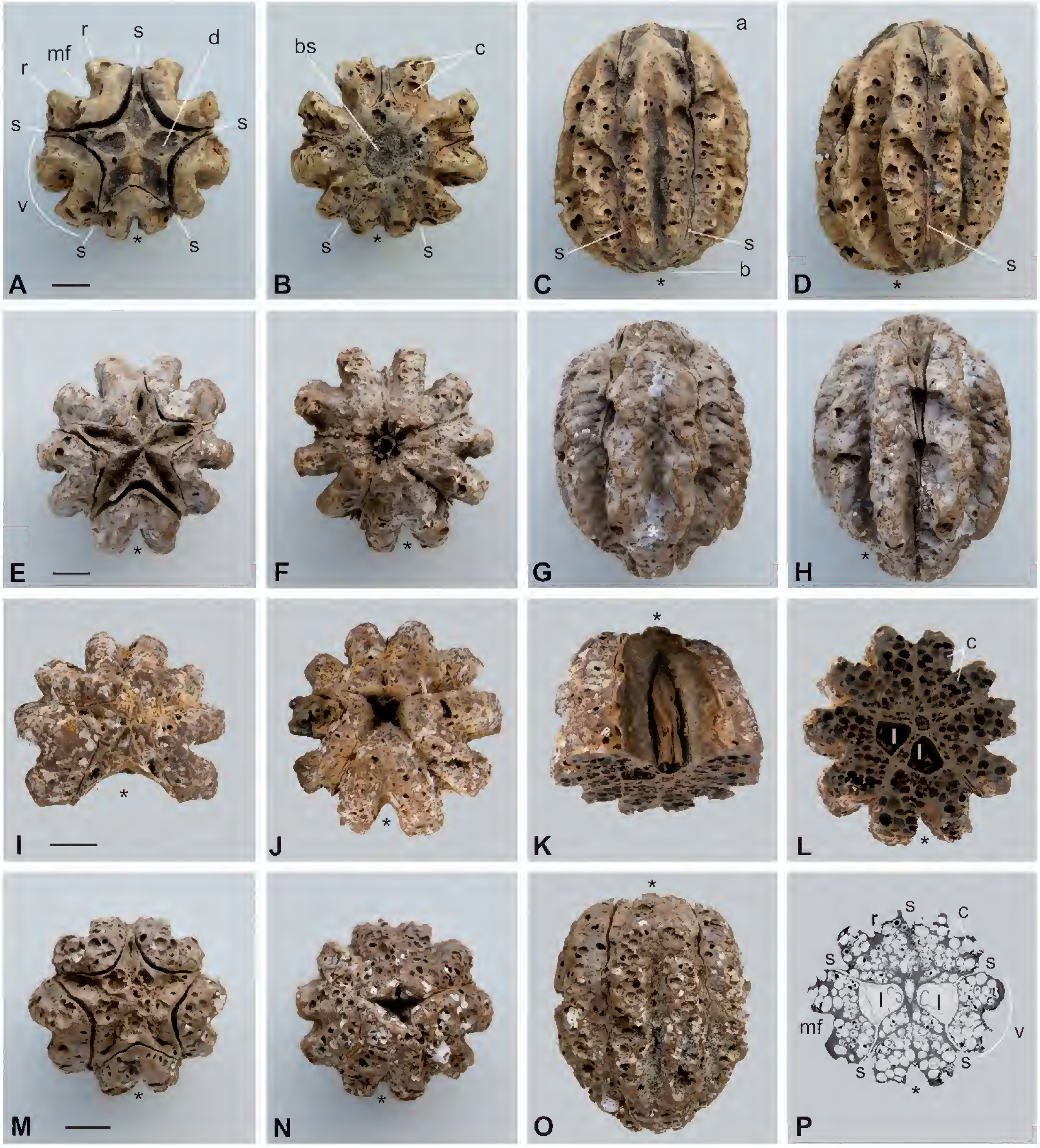

Fig. 1. Endocarps of *Sacoglottis* cf. *costata* (Humiriaceae). First column (A, E, I, M): view of apex; second column (B, F, J, N): view of base; third column (C, G, K, O): view of median furrow on valve (C, G, O) or seed remains (K); fourth column: view of septum (D, H) or section (L, P). Corresponding valves in different photographs of the same specimen are indicated with an asterisk (*). a = apex, b = base, bs = basal scar, d = one of five depressions around apex, l = locule, mf = median furrow on valve, r = one of two ridges on valve, c = cavity, s = septum, v = valve. Scale bar = 10 mm. A–D, Specimen #5, from Yerseke, Netherlands. E–H, Specimen #4, from Palm Beach County, Florida, U.S.A. I–L, Specimen #7, from Bermuda, U.K. (photographed by Bob & Helle Patterson). This specimen is cross-sectioned, with one valve removed from upper half of endocarp (Fig. 1I) showing seed remains (Fig. 1K). Fig. 1L represents the lower half, showing two adjacent fertile locules and many small cavities (compare with Fig. 1P, 3D). M–P, Specimen #9, from South Padre Island, Texas, U.S.A. Fig. 1P shows a micro-CT cross-section showing two opposite fertile locules and many small cavities (compare with Fig. 1L, 3D).

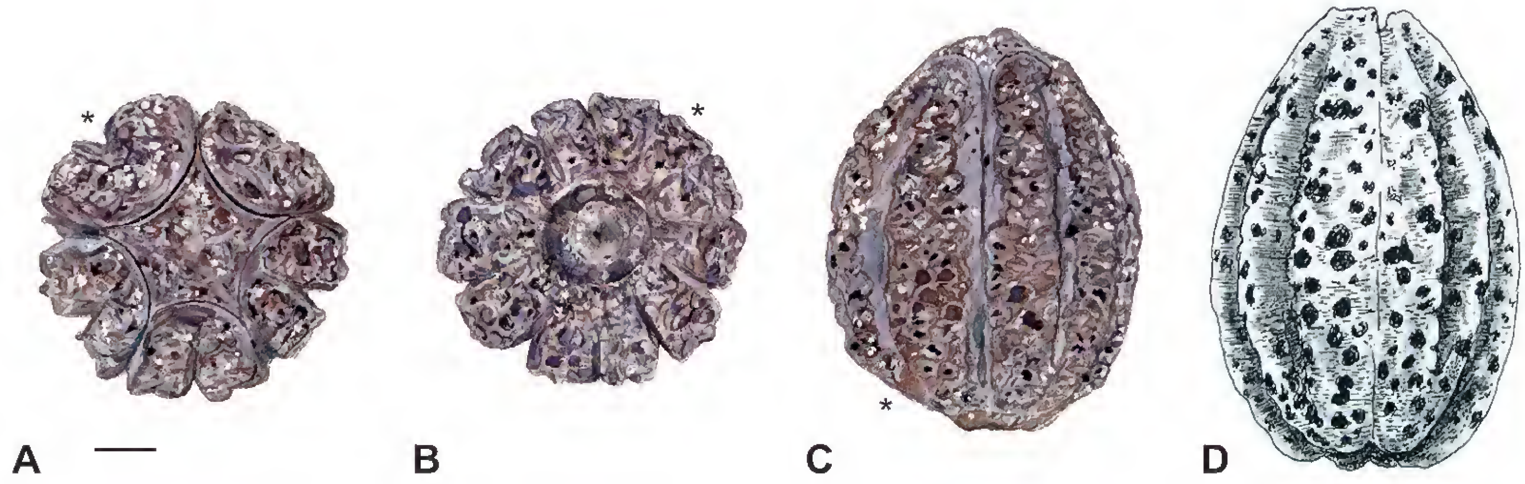

Fig. 2. Endocarps of *Sacoglottis* cf. *costata* (Humiriaceae). Scale bar = 10 mm. A–C, Specimen #2, painted by Izumi Hanno, from unknown location. Corresponding valves are indicated with an asterisk (*). A, view of apex. B, view of base. C, view of septum (compare with Fig. 1D, 1H, 2D). D, Specimen #1, from SE coast of Florida, U.S.A. (from Gunn & Dennis 1976; drawing by Pamela J. Paradine), view of septum (compare with Fig. 1D, 1H, 2C).

Fig. 2D in present paper). This drawing was included in a plate illustrating disseminules of mahogany (*Swietenia mahagoni* (L.) Jacq., Meliaceae) from the southeastern coast of Florida, U.S.A. However, after checking mahogany fruits it was learned that neither the drawing nor the sea-bean from the Netherlands could possibly be this species or any other species of the family Meliaceae.

After some research, the sea-bean was identified as an endocarp[1] from a fruit of a Humiriaceae species. A well-known sea-bean from this almost completely Neotropical family is the blister pod: *Sacoglottis amazonica* Mart. (Fig. 3A–D). This endocarp, with crowded large globular cavities (blisters), is "one of the most common tropical drift seeds found on Florida east coast beaches" (Perry & Dennis 2003:79). It is found on beaches all around the North Atlantic Ocean and has occasionally also been collected in northwestern Europe (Devon, Ireland, Scotland; Guppy 1917; Nelson 2000). However, the unknown, distinctly furrowed endocarp does not resemble the endocarp of *S. amazonica*: the latter is small, its cavities are large, and its surface is bullate with only shallow and irregular furrows (Fig. 3A–D). The endocarp of *Vantanea guianensis* Aubl. (Humiriaceae), mentioned by Gunn and Dennis (1976) as being "not found too far beyond their northern South America homeland," does not compare either. The unknown endocarp was provisionally assigned to the genus *Duckesia* Cuatrec. (Humiriaceae), on the basis of the large size, the (supposed) presence of foramina (holes) in the septa near the apex and medium-sized cavities visible at the surface of the valves, and comparison with material published by Herrera et al. (2010). Fabiany Herrera (pers. comm. 2012) agreed, but advised to section the endocarp in order to confirm this affinity. Consulting "sea-beaner" Ed Perry prompted the reply "This is *Sacoglottis gabonensis*! … related to blister pod …, but much rarer in drift." Following the accompanying link to *Sacoglottis gabonensis* on the website www.seabean.com provided photographs of two furrowed, undoubtedly conspecific endocarps from Florida, one from Palm Beach County (Fig. 1E–H), the other from Lignumvitae Key. A photograph of an additional specimen (Fig. 1I–L) from Bermuda was sent with Ed's reply. The African *Sacoglottis gabonensis* (Baill.) Urb. is the only non-American species of Humiriaceae. Endocarps of this locally common species are often found floating in rivers and on sea shores in the western part of tropical Africa (Cuatrecasas 1961). *S. gabonensis* might be closely related to *S. amazonica* (see also Renner 2004) and produces similar though smaller and more globular endocarps, which differ from the unknown endocarp. A request by Ed Perry via Facebook ("Sea Beans" group) generated donations of two more specimens of the unknown endocarp, one from Volusia County, Florida, and one (Fig. 1M–P) found stranded on South Padre Island, Texas, U.S.A. In 2011 coauthor Izumi Hanno painted an unidentified sea-bean in the Gunn/Dennis collection. This specimen (Fig. 2A–C) clearly represents the unknown

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[1] An endocarp is the woody ("stony") inner layer of the fruit wall of a drupe, together with the mesocarp (middle layer) and exocarp (outer layer, also called epicarp) making up the entire fruit wall.

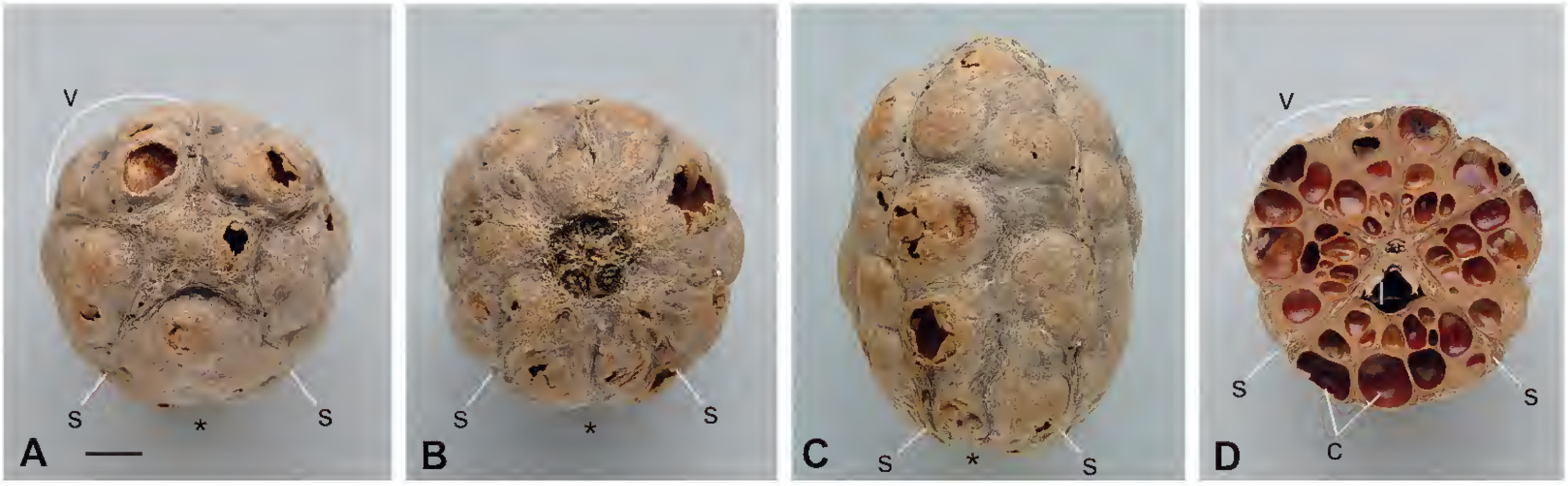

Fig. 3. Endocarp of *Sacoglottis amazonica* Mart. (Humiriaceae) from unknown location (#133, carpological collection of the Utrecht herbarium in Naturalis Biodiversity Center, Leiden, Netherlands). Corresponding valves are indicated with an asterisk (*). l = locule, c = cavities, s = septum, v = valve. Scale bar = 10 mm. A, view of apex. B, view of base. C, view of valve (compare with Fig. 1C, 1G, 10). D, cross-section showing one fertile locule and relatively few large cavities (compare with Fig. 1L, 1P).

endocarp but deviates in size, shape, and details from the one depicted in Gunn and Dennis (1976, Fig. 71B; Fig. 2D in present paper). Therefore, it is assumed that two specimens might be or have been present in the Gunn/Dennis collection[2]. In 2014 a specimen was reported by Jenifer Mina. She found it (without data) on the 'sharing table' during the Nineteenth Annual International Sea-Bean Symposium and Beachcombers' Festival in October 2014 at Cocoa Beach, Florida. According to Ed Perry, it might have been collected in Texas by George Wolf (Pasadena, Texas), who donated so much to put on the sharing table. Correspondence with the collectors/owners of the furrowed endocarps led to enthusiastic response and cooperation, so that (data of) ten specimens are now available. The purpose of the present paper is to describe them and to assess their status within the Humiriaceae.

MATERIAL AND METHODS

Ten specimens of the furrowed endocarp are known (Table 1, Fig. 4), of which one (#3) is probably lost (collection Cathie Katz, died 2001; seen by Ed Perry; no further data available). The present location of the other specimens is cited in Table 1 in the column "collection."

The CT image (Fig. 1P) was made with a Bruker SkyScan1172 high-resolution microCT (Naturalis Biodiversity Center, Leiden, Netherlands).

RESULTS

The furrowed endocarps available for further study (#4–10; Table 1, Fig. 1A–P) are 54–72 mm long, 40–62 mm wide (avg. 63.4 and 50.0 mm) and have an ovoid, ellipsoid to almost globular, or obovoid shape (length/width ratio 1.02–1.42, avg. 1.28). Some specimens (especially #4 and #5) are slightly asymmetrical due to the larger size of the valves covering fertile locules. The base contains a depressed, circular to pentagonal innervation scar, while the apex shows a bulging, 5-rayed star (= top of axis with radiating septa) with a 2–6 mm deep, radially oblong depression in each septum. At the surface of the endocarp, the five septa extend towards the base as 0.3 to ca. 1 mm wide irregular ridges, each at the bottom of an oblong, up to 5 mm deep, and 15 mm wide furrow (Fig. 1C, D). Above the base, the septa diverge into the area around the basal innervation scar. The valves range from oblong to elliptical in longitudinal view, slightly shorter than the endocarp itself and up to 30 mm wide at the equator. Valves covering fertile locules are slightly larger than those on the infertile ones. Only the basal part of each valve is connected with

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[2] The Gunn/Dennis collection contains the material that was the basis for the records in Gunn and Dennis (1976). At present, the collection is in the possession of coauthor Izumi Hanno. It is in storage (Jacksonville, FL, USA) and temporarily inaccessible.

TABLE 1. List of specimens, collection data and features of the furrowed endocarp (*Sacoglottis* cf. *costata*).

#	locality	year	source/collector	collection	L × W (mm)	shape	Fig.
1	SE coast of Florida, U.S.A.	≤ 1976	Gunn & Dennis (1976)	Hanno	ca. 60 × 40	ovoid	2D
2	?	?	Gunn/Dennis collection	Hanno	c. 64 × 49	ovoid	2A–C
3	?	≤ 2000	Cathie Katz / Ed Perry	lost?	?	?	-
4	Palm Beach County, FL, U.S.A.	ca. 2003	Paul Mikkelsen	L	67 × 54	ellipsoid	1E–H
5	Yerseke*, Netherlands	ca. 2007	Theo Lambrechts	L	62 × 47	ovoid	1A–D
6	Lignumvitae Key, FL, U.S.A.	2009	Mike Romance	Romance	63 × 62	± globular	-
7	Bermuda, U.K.	"some y. ago"	Bob Patterson	Patterson	64 × 45	ellipsoid	1I–L
8	Volusia County, FL, U.S.A.	2013	Kim Lincicome	FLAS	62 × 46	ellipsoid	-
9	South Padre Island, TX, U.S.A.	2013	Linda Butcher	BRIT	54 × 45	obovoid	1M–P
10	Texas?, U.S.A.	≤ 2014	George Wolf? / Jenifer Mina	L	72 × 51	obovoid	-

Note. The specimens are listed more or less in order of collecting. Collection: BRIT = Botanical Research Institute of Texas, Fort Worth, Texas, U.S.A.; FLAS = University of Florida Herbarium, Florida Museum of Natural History, Gainesville, Florida, U.S.A.; L = Naturalis Biodiversity Center, Leiden, Netherlands. Collections Hanno, Patterson and Romance: see author addresses. L = length, W = Width. * Specimen #5 was found in Yerseke, Netherlands, among material dredged from the Middeldiep, along the nearby North Sea coast.

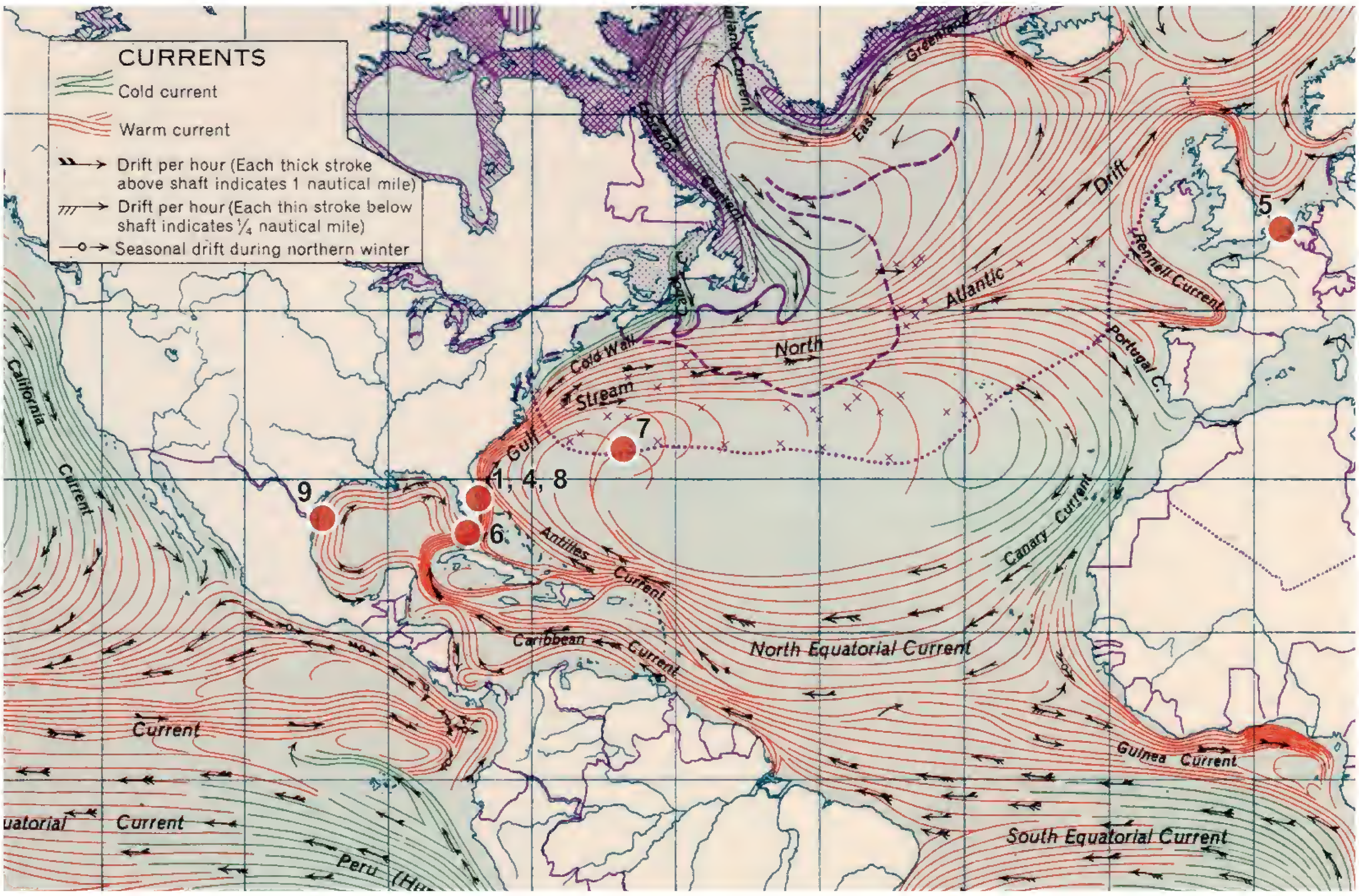
CURRENTS
Cold current
Warm current
Drift per hour (Each thick stroke above shaft indicates 1 nautical mile)
Drift per hour (Each thin stroke below shaft indicates ¼ nautical mile)
Seasonal drift during northern winter
East Greenland
Labrador Current
Cold Wall
Gulf Stream
North Atlantic Drift
Rennell Current
Portugal C.
Canary Current
Antilles Current
Caribbean Current
North Equatorial Current
Guinea Current
South Equatorial Current
California Current
Current
uatorial Current
Peru (Hu
1, 4, 8
5
6
7
9

FIG. 4. Map showing localities of stranded specimens of *Sacoglottis* cf. *costata* (Humiriaceae). #1: SE coast of Florida, U.S.A.; #4: Palm Beach County, Florida, U.S.A.; #5: Yerseke, Netherlands; #6: Lignumvitae Key, Florida, U.S.A.; #7: Bermuda, U.K.; #8: Volusia County, Florida, U.S.A.; #9: South Padre Island, Texas, U.S.A. Localities of #2, #3, and #10 unknown. The localities are plotted on a map originally compiled to show cold and warm sea currents and the extent of sea ice in the North Atlantic Ocean (United States Army 1943).

the axis of the endocarp (Fig. 1A–C). Each valve shows a median furrow up to 10 mm deep and 10 mm wide at the equator. Thus a total of ten distinct longitudinal furrows mark the surface of the endocarp from base to apex. Alternatively, the surface may be described as beset with ten wide conspicuous ribs (two on each valve). Cross-sections of three endocarps are available: a physical section of specimen #7 (Fig. 1L) and micro-CT scans of specimens #5 and #9 (Fig. 1P). All sections show a 5-radiating axial structure with septa narrowing outwards. Specimens #5 and #9 contain two opposite fertile locules, while specimen #7 has two adjacent fertile locules, which are more or less obtusely triangular in cross-section, each containing the remains of an oblong seed. Septa and valves contain many globular cavities, up to 4 mm in diameter. There are no traces remaining of the exocarp and mesocarp.

Some specimens are worn, especially #5. Specimens #2 and #4–10 are sparsely to densely covered with marine epibionts, including barnacles, small bivalves, bryozoans, calcareous tube worms, foraminifers, hydroids, and coralline red algae.

DISCUSSION

Comparison with the family Humiriaceae

The family Humiriaceae belongs to the order Malpighiales and comprises eight genera (*Duckesia* Cuatrec., *Endopleura* Cuatrec., *Humiria* Aubl., *Humiriastrum* (Urb.) Cuatrec., *Hylocarpa* Cuatrec., *Sacoglottis* Mart., *Schistostemon* (Urb.) Cuatrec., and *Vantanea* Aubl.) with about 50 species. The gynoecium in Humiriaceae is syncarpous and usually 5-merous. The fruit is a pea-sized to mango-sized drupe with a single, multi-seeded woody endocarp, which is very distinctive and one of the outstanding features of the family (Cuatrecasas 1961; Herrera et al. 2010). The endocarp shows five septa and five valves (up to 8 and 10 in *Vantanea* and *Humiria)*, but most with only one or two locules, in each of which a single seed develops, except in the genus *Humiria* that has two seeds per locule. The septa radiate from the axis of the endocarp. Together, the axis and septa make up a rigid and resistant frame from which the valves of the fertile locules separate during germination. The endocarps of *Duckesia*, *Humiriastrum* (partially), *Sacoglottis,* and *Schistostemon* contain large (up to 7 mm), globular, ± empty cavities in their septa and valves. Intergeneric differences occur in the relative width of the septa and valves at the surface, the length of the valves, and the surface sculpture of the septa and valves (see below). The features mentioned above and combined with the resistant nature of the endocarps, make the fruits of Humiriaceae readily identifiable objects in dispersed state (e.g., fossils, sea-beans). The woody endocarps of species that occur on river banks and in temporarily flooded forests (e.g., *S. amazonica*, *S. gabonensis*) have a good chance of being dispersed by water because the cavities provide them with extra buoyancy.

In most Humiriaceae endocarps, valve width at the surface (measured at the equator) is equal to or smaller than that of the septa (Cuatrecasas 1961; Herrera et al. 2010). In *Humiriastrum*, valve width is occasionally larger than septum width, but in this genus the valves are only up to half as long as the endocarp and are located near the apex of the endocarp. In *Sacoglottis* and *Schistostemon* the valves are nearly as long as the endocarp and the septa are very thin or hardly or not visible at the surface, so that the valves are very wide, sometimes even adjacent. This exact condition is present in the furrowed endocarps analyzed in this study. *Sacoglottis* and *Schistostemon* are differentiated from each other by a flower character (stamen number: 10 and 20, respectively), but their endocarps are indistinguishable (Cuatrecasas 1961). In their morphological cladistic analysis, Herrera et al. (2010) found that *Sacoglottis* and *Schistostemon* are sister groups, and they consider that the genera should be reduced to subgenera of the genus *Sacoglottis*. Isolated endocarps with very thin septa, including the furrowed endocarps described in the present study, might then be identified as belonging to *Sacoglottis* s.l. (sensu lato, in broad sense: *Sacoglottis* and *Schistostemon* together). Additional features supporting the assignment of the furrowed endocarps to *Sacoglottis* s.l. are the presence of up to 4 mm large cavities throughout the endocarp and the absence of apical foramina (holes) in the septa. Cavities occur also in *Duckesia* and *Humiriastrum* (partially), but they are only a little larger than 0.7 mm at most (pers. comm. Fabiany Herrera 2012). Apical foramina are also absent in *Hylocarpa* and *Vantanea*, but endocarps of these genera are very different from the furrowed endocarps (e.g., valves equal or narrower than septa). Sometimes, apical foramina seem to be present in the furrowed endocarps (e.g., in specimen #4; Fig. 1E), but actually these holes represent cavities surfacing in the depressions near the apex.

Comparison with extant *Sacoglottis* s.l.

Sacoglottis s.l. comprises 20 species (Cuatrecasas 1961, 1972, 1990; Sabatier 1987; Burger & Zamora Villalobos 1991, Zamora Villalobos 2007). All known endocarps of *Sacoglottis* s.l. species are not or are only inconspicuously furrowed. Although inclusion of the furrowed endocarps in *Sacoglottis* s.l. is well-supported, matching them with any of the known endocarps of the species in this group is therefore impossible. Furthermore, the furrowed endocarps are relatively large: 54–72 mm (avg. 63.4) long. Only *Schistostemon retusum* (Ducke) Cuatr. has larger endocarps: 70–80 mm long (Lorenzi 2002)[3]. *Sacoglottis amazonica* (Fig. 3A–D) produces the next largest endocarps: 20–60 mm long (Gunn & Dennis 1976), but normal-sized specimens are about 40 mm long (Perry & Dennis 2003).

A few rare species are known from flowering material only: *Sacoglottis maguirei* Cuatrec. and *Schistostemon auyantepuiense* Cuatrec. *Sacoglottis maguirei* is a xeromorphic endemic from Venezuela (Amazonas, frequent at top of Cerro Yapacana, 1200 m alt.; Cuatrecasas 1961). The single known specimen of *S. maguirei* has flowers and very young fruits (see also Cuatrecasas & Huber 1999, Fig. 540). Theoretically (by lack of data), the furrowed endocarps might belong to *S. maguirei*. Cerro Yapacana is adjacent to the Orinoco, so transport of endocarps by that river to the Caribbean Sea might occur. Mature fruits of *S. maguirei* might still be collected in the Yapacana National Park. For the time being, some evidence is provided by *Sacoglottis* sp. A (Zamora Villalobos 2007), an endemic from Costa Rica (Cordillera de Talamanca, 440 m alt.). This species is known from one fruiting collection, bearing globular to ellipsoid, ca. 35 × 29 mm large fruits. *Sacoglottis* sp. A is possibly related to *S. maguirei* (Zamora Villalobos 2007). If related, the small size of its fruits would separate the furrowed endocarps from *S. maguirei*.

Schistostemon auyantepuiense is an endemic from Venezuela (Bolívar, near Guayaraca, 900–1100 m alt.). It is a xeromorphic species very similar to *Schistostemon fernandezii* Cuatrec. from the same area (according to Cuatrecasas & Huber 1999 even questionably different) and closely related to *Schistostemon reticulatum* (Cuatrecasas 1961). Fruits of *S. reticulatum* measure about 30 mm (pers. comm., Pedro Jordano 2014). If *S. auyantepuiense* is indeed closely related to *S. fernandezii*, it is expected to have fruits like those of *S. fernandezii* (see Cuatrecasas & Huber 1999, Fig. 544, and Herrera et al. 2010, Fig. 2O), i.e., with a small, hardly or not furrowed endocarp. Therefore, conspecifity of the furrowed endocarps with *S. auyantepuiense* and/or *S. reticulatum* is less probable.

Comparison with fossil *Sacoglottis* s.l.

Herrera et al. (2010, 2014) have revised the fossil record of the family Humiriaceae, especially that of its resistant endocarps. They combined several fossil species into *Sacoglottis tertiaria* Berry emend. Herrera, which is now known from Oligocene, Miocene, Pliocene, and Pleistocene deposits in Bolivia, Colombia, Costa Rica, and Panama (see also Lott et al. 2011). Most of the included fossils very much resemble the *Sacoglottis* s.l. endocarps as described above. Their surface is described as slightly bullate. However, the single specimen on which the included *Sacoglottis costata* Reid from the Tertiary of Colombia was based shows five radial depressions around the apex and 15 longitudinal ridges between base and apex. Five ridges are thin and represent the five septa. The remaining ten ridges are arranged in pairs, each pair flanking a deep median furrow on a valve (Reid 1933, plate 14, Figs. 1, 1a, 2, 2a; Fig. 5A–D in present paper). Herrera et al. (2010) interpreted the furrows as the result of abrasion or erosion, but originally the fossil was described as a "beautiful specimen." The wear noticed by Reid refers only to the lack of cellular surface details (Reid 1933). The differences between *S. costata* and the endocarps of extant species of *Sacoglottis* s.l. (especially *S. amazonica*), mentioned and adequately illustrated by Reid (1933), correspond very well with the unusual features of the furrowed endocarp (compare Fig. 1A–P, Fig. 3A–D,

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[3] The material described and illustrated by Lorenzi (2002) originates from the coastal region of southern Bahia (Brazil). Material from Amazonas (Brazil), Colombia and Venezuela described by Ducke (1938, Fig. 2d), Cuatrecasas (1961, Fig. 31j) and Herrera et al. (2010, Fig. 2D) contained much smaller, though apparently mature endocarps (globular, 26–34 mm diameter). The endocarps illustrated by Lorenzi (2002) do not show any characteristics of *Sacoglottis* s.l. or even Humiriaceae (valves, septa, cavities), but this may be due to their freshly peeled state.

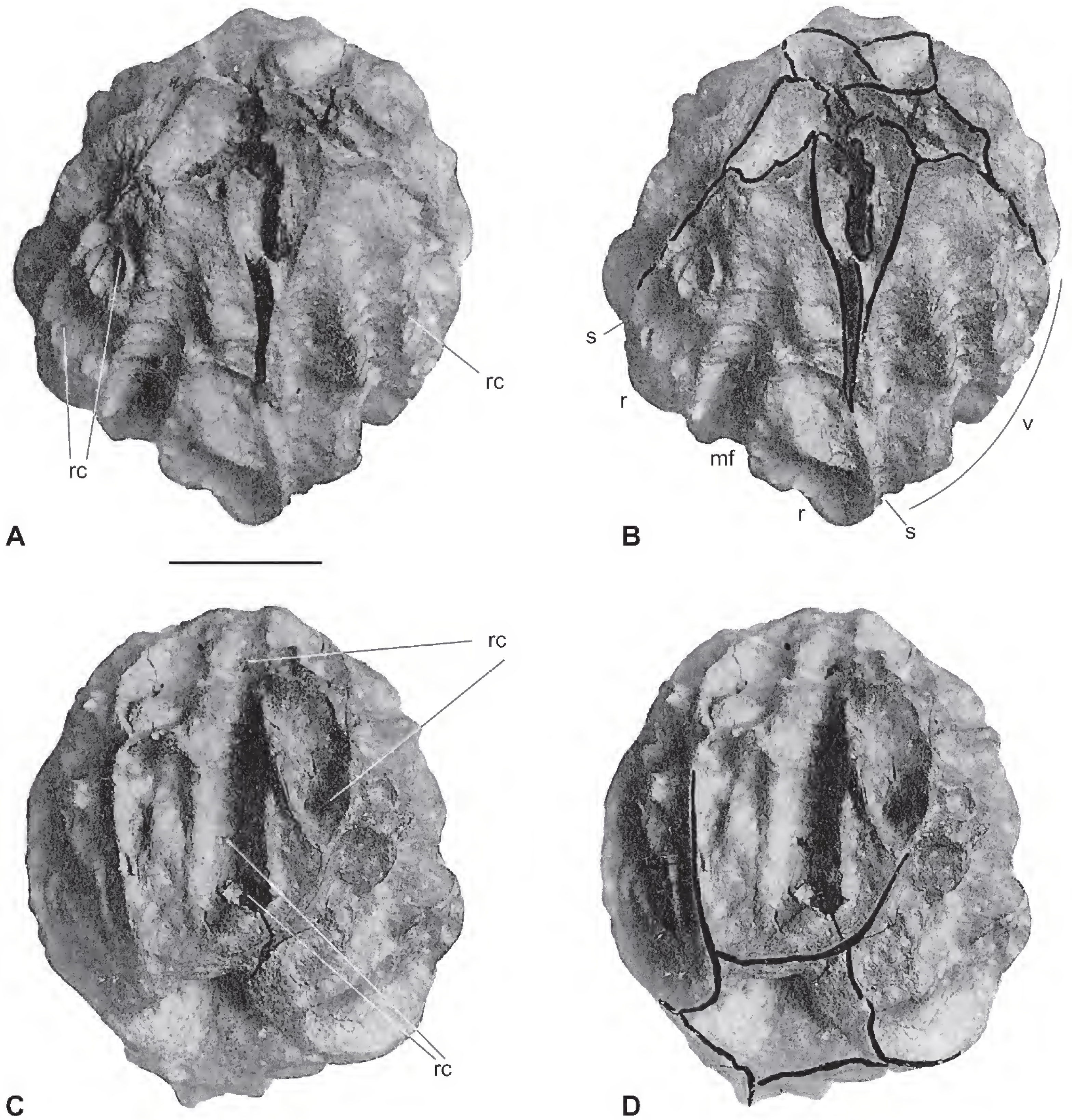

Fig. 5. Only known specimen of the fossil endocarp *Sacoglottis costata* Reid (original figure from Reid 1933; symbols added in B). mf = median furrow on valve, r = one of two ridges on valve, rc = (resin) cavity, s = septum, v = valve. Scale bar = 10 mm. A, oblique view of apex. B, as A, with lines accentuating the position of septa (boundaries of valves) around the apex. C, oblique view of base. D, as C, with lines accentuating the position of septa (boundaries of valves) around the base.

and Fig. 5). The only remaining difference is size: the fossil measures 30 × 26 mm, which is about half as large. Incidentally, the size of *S. amazonica* endocarps shows a wide range: from 20 to 60 mm long (Gunn & Dennis 1976). Of course, the state of preservation also distinguishes the fossil from the recent furrowed endocarps. The size difference may partly be explained by the fossilization process, e.g., shrinkage by coalification. The state of the fossil was characterized as "highly carbonized, close, hard and glossy in texture, and quite black" and said to "break with a conchoidal fracture." This was regarded by Reid (1933) as pointing to considerable antiquity, but the actual age of the fossil is unknown. Unfortunately, the specimen could not be traced in the Reid collections in the Natural History Museum in London (pers. comm. Peta Hayes 2014).

The ribbed fossil endocarps from the Neogene of Colombia described by Wijninga (1996) as type T295 (*Humiriastrum*) are small (10–21 × 8–18 mm) and their septa are wider than the valves and therefore do not resemble the furrowed endocarp. According to Herrera et al. (2010) the fossils represent the genus *Duckesia*.

Origin

The furrowed endocarp described here is not the first sea-bean known earlier than its producer. An endocarp of *S. amazonica* (blister pod) was described and illustrated by Clusius (1605, libr. II:45, as *Fructus I. Iac. Plateau*). It was given to him by Jacques Plateau, an apothecary from Tournai (Doornik) in Belgium, who also provided Clusius with data of armadillos (Egmond 2009; Mason 2009). Thus, Plateau had links with the Neotropics, and according to Nelson (2000) Clusius' blister pod was not a European sea-bean. Sloane (1696:214) did mention *S. amazonica* as a sea-bean (*Fructus exoticus cinereus, cum lineis & tuberculis duris*) from Jamaica and also from Jamaica and Europe (Sloane 1725:186): "This is frequently cast up on the Shores of this Island by the Waves, and is one of those Fruits thrown on the Northwest Islands of Scotland, by the Seas". However, *S. amazonica* as a botanical species was described much later by Martius (1827), while its stranded endocarps from Jamaica were identified as *S. amazonica* only in 1889 (Guppy 1917; Cuatrecasas 1961).

It is possible to speculate about the origin of the furrowed endocarps. The five specimens stranded in Florida indicate that the Caribbean Current might have been the way of transport (Fig. 4). This would imply that the parent species of the furrowed endocarp, like *Sacoglottis amazonica*, grows somewhere in northeastern South America, within the reach of river systems like the Amazon, Orinoco, Magdalena, and Atrato Rivers. Transport from the Caribbean Current into the Gulf of Mexico to Bermuda and via the Gulf Stream and the North Atlantic Drift to Europe is possible. Wherever occurring, the producer of the furrowed endocarps might be rare and threatened. In earlier times, its fruits might have been dispersed by a presently extinct megafauna, as described by Jordano (2004) and Guimarães et al. (2008) for several other large-fruited Neotropical species, including the humiriaceous *Duckesia verrucosa* (Ducke) Cuatr. and *Endopleura uchi* (Huber) Cuatr. In Africa, large mammals (e.g., elephants) are still known to forage for fruits of *Sacoglottis gabonensis* (White 1994; Morgan 2009).

CONCLUSIONS

The furrowed endocarps described herein are allocated to *Sacoglottis* s.l. (sensu lato, in broad sense: *Sacoglottis* and *Schistostemon* together).

The furrowed endocarps show a unique feature (distinct furrows) and cannot be matched with any described endocarp of an extant *Sacoglottis* s.l. species. Theoretically, they might belong to *Sacoglottis maguirei* or *Schistostemon auyantepuiense*, two rare species of which fruits are unknown. However, endocarps of (possibly) related species (*Sacoglottis* sp. A and *Schistostemon fernandezii*, respectively) are different from the furrowed endocarps. Therefore, the endocarps of *S. maguirei* and *S. auyantepuiense* are suspected to be different from the furrowed endocarps too. This should be checked in the field.

The furrowed endocarps are most similar to the fossil *Sacoglottis costata*, which is based on a single specimen of unspecified Tertiary age from Colombia. *Sacoglottis costata* is distinct from the fossil species *S. tertiaria*. Apart from the state of preservation and the size difference, it is difficult to define a distinguishing characteristic difference between the extant furrowed endocarps and the fossil *S. costata*. Therefore, we do not erect a new species, but prefer to indicate the furrowed endocarps as *Sacoglottis* cf. *costata*. It is stressed that the resemblance between *Sacoglottis* cf. *costata* and *S. costata* is based on surface characters; knowledge of the internal structure of the *S. costata* specimen might support affinity.

If the furrowed endocarps (*Sacoglottis* cf. *costata*) do not belong to one of the incompletely known species of *Sacoglottis* s.l., we believe that an undescribed species, producing *costata*-like endocarps, exists somewhere in northern South America. In view of the unusual morphology of the endocarps, this species is expected to deviate distinctly from the species of *Sacoglottis* s.l. known at present. As common name of *Sacoglottis* cf. *costata*, "furrowed blister pod" is proposed.

ACKNOWLEDGMENTS

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BOOK NOTICE

E. Charles Nelson & David J. Elliott. 2015. **The Curious Mister Catesby.** (ISBN-13: 978-0-8203-4726-4, hbk). University of Georgia Press, Main Library, Third Floor, 320 South Jackson Street, Athens, Georgia 30602, U.S.A. (**Orders:** www.ugapress.org, 1-800-266-5842). $49.95 US, 456 pp., 238 paintings/illus./photos/maps, 8" × 11".

From the publisher: In 1712, English naturalist Mark Catesby (1683–1749) crossed the Atlantic to Virginia. After a seven-year stay, he returned to England with paintings of plants and animals he had studied. They sufficiently impressed other naturalists such that in 1722 several Fellows of the Royal Society sponsored his return to North America. There Catesby cataloged the flora and fauna of the Carolinas and the Bahamas by gathering seeds and specimens, compiling notes, and making watercolor sketches. Going home to England after five years, he began the twenty-year task of writing, etching, and publishing his monumental *The Natural History of Carolina, Florida, and the Bahama Islands.*

Mark Catesby was a man of exceptional courage and determination combined with insatiable curiosity and multiple talents. Nevertheless no portrait of him is known. The international contributors to this volume review Catesby's biography alongside the historical and scientific significance of his work. Ultimately, this lavishly illustrated volume advances knowledge of Catesby's explorations, collections, artwork, and publications in order to reassess his importance within the pantheon of early naturalists.

E. Charles Nelson is a botanist who served for two decades as a Horticultural Taxonomist at the National Botanic Gardens in Glasnevin, Dublin. He served as Honorary Editor of Archives of Natural History (1999–2012) and has written or edited, singly or collaboratively, nearly forty books. His most recent title is *Shadow among Splendours: Lady Charlotte Wheeler-Cuffe's Adventures among the Flowers of Burma, 1897–1921.*

David J. Elliott is founder, chairman, and now Honorary Trustee of the Kiawah Island Natural Habitat Conservancy. He has been executive director of the Catesby Commemorative Trust since 2002.

A SURVEY OF THE WOODY AND CLIMBING PLANTS OF THE REFUGIO DE AVES DR. ALEXANDER SKUTCH, "LOS CUSINGOS," PÉREZ ZELEDÓN CANTON, COSTA RICA

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ABSTRACT

Los Cusingos is located in southern Costa Rica, near San Isidro de El General, and occupies an area of 77 ha ranging in elevation from 650 to 750 m. The refuge was established by the Tropical Science Center on property formerly owned by Alexander F. Skutch, who was well known for his research in bird behavior and for his many books and journal articles on natural history and philosophical topics. Los Cusingos contains one of the largest remaining tracts of primary forest in the northern portion of the valley of the Río General. A botanical survey of the site between 2007 and 2010 resulted in the documentation of 314 species of woody and/or climbing plants in 217 genera and 84 families. There were 7 species of pteridophytes, 18 species of monocots, and 289 species of dicots. Of the dicots, 57 species were classified as vines, 50 as terrestrial shrubs, 6 as epiphytic shrubs, 5 as parasitic shrubs, 154 as treelets or trees, and 17 as emergent trees. Included in the species list are 16 species that were naturalized or with the potential to become naturalized. Additional non-native species were present in the Pamela Lankester Garden. Of the native species, ten are listed as endangered or threatened in Costa Rica. The Tropical Premontane Wet forest at Los Cusingos is a remnant forest representing a mid-elevation community type that was once widespread in the Río General valley, and contains a number of species that are disjunct from populations found in forests of the Osa Peninsula region. Los Cusingos is included within the Alexander Skutch Biological Corridor, which was established by the Tropical Science Center. The Los Cusingos preserve is a focal point of work to develop this corridor project and to establish working relationships with the local people to encourage their assistance in protecting the remaining resources of the area.

RESUMEN

La reserva Los Cusingos se encuentra en la zona sur de Costa Rica, cerca de San Isidro de El General, y ocupa una superficie de 77 hectáreas, entre 650 y 750 m.s.n.m. Fue establecida por el Centro Científico Tropical en la propiedad que anteriormente perteneció a Alexander F. Skutch, bien conocido por sus investigaciones sobre el comportamiento de las aves y por sus numerosos libros y artículos de revistas acerca de la historia natural y de temas filosóficos. En Los Cusingos se encuentra una de las mayores extensiones de bosque primario aún presente en la parte norte del valle del Río General. El presente estudio se realizó entre 2007 y 2010 resultando la documentación de las 314 especies de plantas leñosas y/o trepadoras pertenecientes a 217 géneros y 85 familias. Se documentan 7 especies de pteridofitas, 18 especies de monocotiledóneas, y 289 especies de dicotiledóneas. De las dicotiledóneas, 57 especies fueron clasificadas como trepadoras, 50 como arbustos terrestres, 6 como arbustos epífitos, 5 como arbustos parásitos, 154 como arbolitos o árboles, y 17 como árboles emergentes. Incluidas en la lista hay 17 especies naturalizadas o con potencial para naturalizarse. Además, se incluyen algunas especies no nativas presentes en el jardín Pamela Lankester. De las especies nativas, 10 figuran como amenazadas o en peligro de extinción para Costa Rica. El Bosque Húmedo Premontano Tropical (bhp-T) de los Los Cusingos representa el tipo de comunidad de elevación media que alguna vez cubrió la mayor parte del valle del Río General, y contiene especies que todavía forman parte de las comunidades boscosas de la Península de Osa. La reserva Los Cusingos se incluye dentro del Corredor Biológico Alexander Skutch, establecido por el Centro Científico Tropical. La reserva Los Cusingos es un punto focal para desarrollar el corredor biológico y para establecer relaciones de trabajo con las comunidades locales buscando alentar su apoyo a la protección de los restantes recursos de la zona.

INTRODUCTION

Refugio de Aves Dr. Alexander Skutch, "Los Cusingos," hereafter referred to as Los Cusingos, is a 77 hectare preserve in southern Costa Rica. It is managed by the Tropical Science Center (TSC), which is headquartered in San José. Numerous bird studies have been conducted (more than 300 bird species have been documented) in the sanctuary, but there have been no comprehensive floristic studies (sporadic plant collections were made by Alexander Skutch and others). Los Cusingos is one of the last remaining forest fragments in this now

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largely agricultural region of the valley of the Río General, an area that has been heavily impacted by conversion of forests for agriculture (especially coffee, sugar cane, and pineapple), as well as for housing and commercial enterprises. The site is also notable for the presence of several large rock formations with Native American petroglyphs.

Visitors and researchers are welcome, and Los Cusingos is being actively promoted as a site for various research and community activities. Researchers are encouraged to develop projects utilizing Los Cusingos, and approval is required through the TSC. Los Cusingos is part of a network of preserves operated by the TSC. This network was formally established in the year 2000 with the goal of conserving tropical forests as well as providing environmental education, research opportunities, natural resources protection, environmental services, and ecological tourism.

The goals of this study were to: 1) conduct a botanical survey focusing primarily on woody plants and climbing plants (excluding Araceae, Bromeliaceae, and Orchidaceae); 2) prepare a species list for the preserve; and 3) broadly describe the different kinds of plant groups present based on habit and community associations.

Dr. Alexander Skutch and Los Cusingos

After receiving a doctorate in botany from John Hopkins University in 1928, Dr. Alexander Skutch worked on a variety of projects in Central and South America, before settling in the 1940s on a farm near San Isidro de El General (Skutch 1980, 1992; Abarca Jiménez 2004; Lewis 2004). He named his farm "Los Cusingos," the local name of a species of toucan, the fiery-billed aracari (*Pteroglossus frantzii* Cabanis). In his early years he supported himself by collecting plant specimens from Costa Rica and South America for other scientists. Many of these plants were new to science, and his collaborators often named the new species in his honor, usually with "*skutchii*," as the epithet. Over his lifetime he produced some 200 scientific articles and 20 books on birds, and another 50 articles and seven books on philosophical and autobiographical topics. His ground-breaking research into avian sociobiology and life history won him a number of national and international honors and awards. His crowning achievement was *A Guide to the Birds of Costa Rica* (Stiles & Skutch 1989), published when he was 85 years old. Toward the end of his life Dr. Skutch made arrangements with the Tropical Science Center to maintain his farm as a bird sanctuary. He passed away in 2004, at the age of 99. Alexander Skutch is buried in an unmarked grave behind his home at Los Cusingos.

Site Description

Los Cusingos is located near the small towns of Quizarrá and Santa Elena, in the San Isidro de El General District, Pérez Zeledón Canton, San José Province, Costa Rica (Figs. 1, 2). It is 14 km (or about 20 minutes driving time) from San Isidro de El General, which is about 3 hours by automobile from San José at a distance of 130 km. Los Cusingos is about 10 km southwest of the peak of Cerro Chirripó, the highest mountain in Costa Rica at 3820 m.

The following climatic data was taken from World Weather Online (2014). In this region the dry season extends from December through April, and the rainy season from May to late November. Rainfall averages are less than 50 mm per month during the dry period, but increases to over 150 mm in May, and reaches highs of around 200 mm or more per month in the rainy season. The annual precipitation at San Isidro de El General is about 2700 mm. The average monthly daytime temperatures are relatively stable, ranging from 27°C during the rainy period to 31°C in the dry period. Nighttime temperatures range from 18 to 19°C, averaging slightly cooler during the dry period. The area of Los Cusingos closely corresponds to the Tropical Premontane Wet Life Zone in the Holdridge Life Zone System (Holdridge 1967; Bolaños et al. 1999; Jiménez-Saa 2013).

The refuge is largely forested, with several streams, but has some open areas with buildings and gardens at the north end of the refuge. The buildings include a visitor's center (at 09°20'22"N; 83°37'43"W), a researchers cabin, and Skutch's house, which he began constructing in the early 1940s and is now restored and maintained as a museum of his life's work. A few other smaller buildings also exist on the property, and more are planned. The area occupied by the buildings and demonstration areas is about one hectare. The remaining 76 hectares are chiefly primary forest. Elevations at Los Cusingos range from 650–750 meters, and several trails

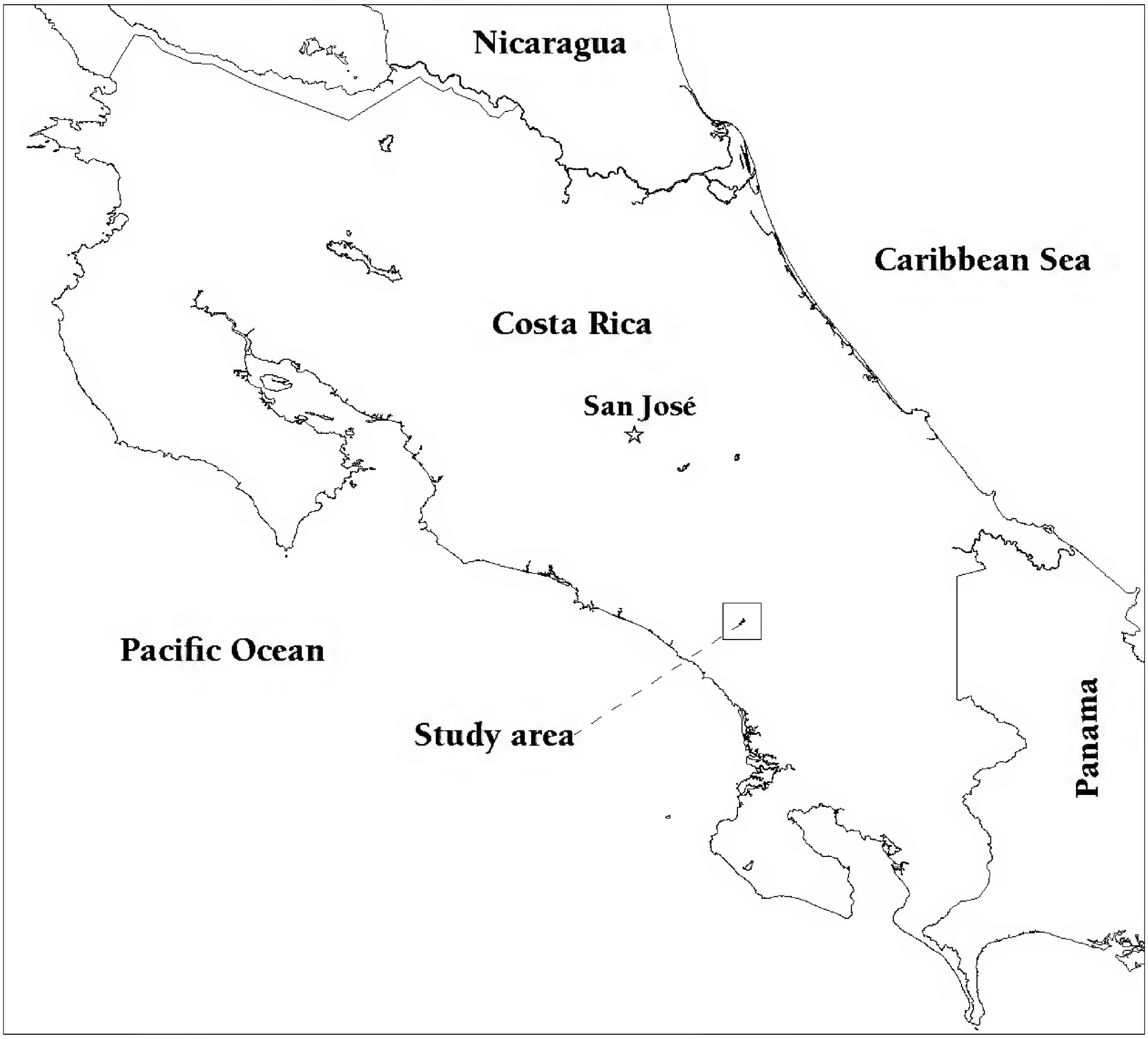
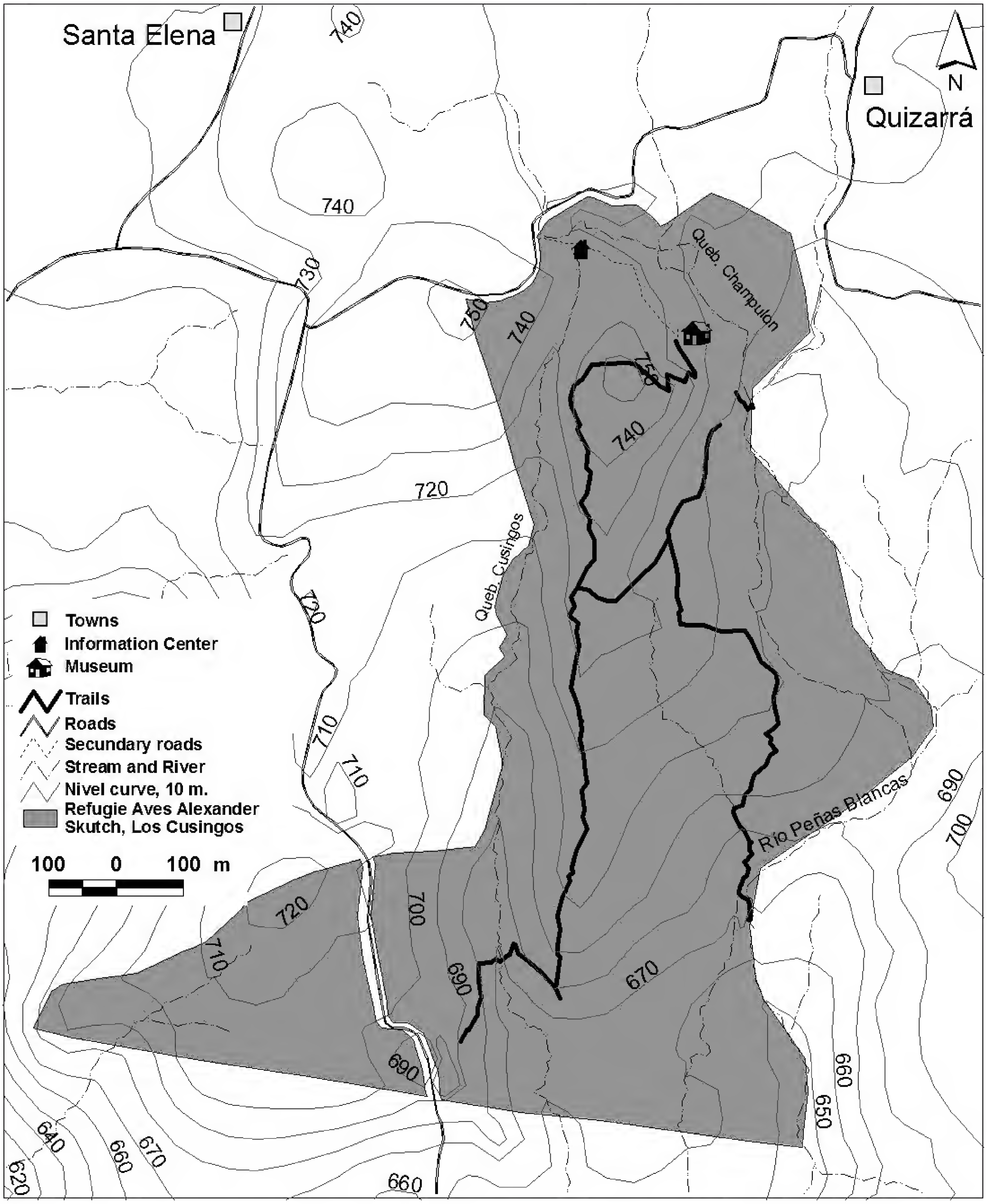


Fig. 1. Location of Refugio de Aves Dr. Alexander Skutch, "Los Cusingos" in San Isidro de El General District, Costa Rica (Tropical Science Center, GIS Department, Vladimir Jiménez).

are maintained (Fig. 2). A trail guide is available for the main loop trail, Sendero Naturalista; it provides color photographs and descriptions of species for 21 stations that are permanently marked along the trail (Jones et al. 2014). The main water course is the Rio Peñas Blancas, which forms most of the eastern boundary of the property. Other smaller streams include the Quebrada Llano, Quebrada Champulon, Quebrada Pejibaye, Quebrada Cusingos, and Quebrada Mapache.

Hammel et al. (2004) noted that these forests in the Río General valley have a floristic composition unique in Costa Rica, often with species more characteristic of the southern Pacific Coast, especially Corcovado National Park. These authors further note that the forests were nearly completely destroyed over the last 60+ years in the valley, but that the few remaining fragments provide evidence that a unique and phytogeographically interesting forest once occupied these mid-range elevations. There have been few studies in Costa Rica of mid-elevation forests; examples include those by Fournier et al. (1985), Wattenberg and Breckle (1995), Homeier et al. (2005), and Cascante Marín et al. (2012). Holdridge et al. (1971) reported studies on a number of forest sites in Costa Rica, including several sites at similar elevation to Los Cusingos, and included information on soils, vegetation features, quantitative vegetation data, and species lists.


Santa Elena
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Queb. Champulon
Queb. Cusingos
Río Peñas Blancas
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650
640
620
Towns
Information Center
Museum
Trails
Roads
Secundary roads
Stream and River
Nivel curve, 10 m.
Refugie Aves Alexander Skutch, Los Cusingos
100 0 100 m

Fig. 2. Map of Refugio de Aves Dr. Alexander Skutch, "Los Cusingos" in San Isidro de El General District, Costa Rica. (Tropical Science Center, GIS Department, Vladimir Jiménez).

Skutch (1980) described his first impressions of the Río General valley on his first visit in 1935 as "an isolated region, surrounded by vast, scarcely broken forests, and easily accessible only by air." In this same book he described his recollections upon first seeing the farm in 1941 that would become Los Cusingos: "What interested me more was the forest … a large tract of unspoiled forest remained, with trees towering up to one hundred and fifty feet, multitudes of palms with slender, towering trunks, orchids and many other epiphytes on the trees, and beneath them many low palms and flowering shrubs, and great-leaved herbs."

Skutch (1980, 1992) specifically mentions many of the species that grew on his property. He noted the larger trees such as palo de leche (*Brosimum utile*), burío (*Heliocarpus* spp.), chumico (*Pourouma* sp.), campana (*Gordonia fruticosa*), candela (*Virola* spp.), cerillo (*Symphonia globulifera*), gallinazo (*Jacaranda* sp.), iri chiricano (*Vantanea barbourii*), mayo trees (*Vochysia* spp.), and *Goethalsia meiantha*. In the understory were guarumo (*Cecropia* spp.), cacique (*Myrciaria floribunda*), palms such as chonta (*Socratea* sp.) and palmito (*Euterpe* sp.) and many species of *Miconia*. Gnarled sotacaballo trees (*Zygia longifolia*) grew along the Rio Peñas Blancas. He noted his disgust for the two most aggressive vines in the forest: the gigantic leguminous vine *Entada gigas* with stems looping high in the canopy from tree to tree like enormous cables, these sometimes 15 inches (38 cm) thick, with pods over a meter long; and the slender vine *Salpichlaena volubilis*, a fern in the Blechnaceae, which formed almost impenetrable thickets in the undergrowth. He also noted ongoing changes in the forest, such as the sharp decrease in numbers of his palmito trees, cut by poachers for their edible "palm hearts," and the aging and loss of some canopy species, such as the campana, and the increase in numbers of the palo de leche. Once settled in Los Cusingos, Skutch devoted his life to his bird studies and to protecting his property, but apparently did not collect many plant specimens from his farm, or compile a comprehensive list of the plant species.

METHODS

Prior to the study, a list of species documented in Pérez Zeledón Canton was obtained from the databases of the Herbario Nacional, San José, Costa Rica, but only about 30 specimens were actually from Los Cusingos. Additional information on species records in the region was gathered from the INBio website (INBio 2007).

Collecting for this project was done by RLJ and HJS from February to May, 2007, in July 2008, and in March 2009; collecting by ACR, HJS, and RLJ occurred in May, 2010. All sections of the refuge were regularly accessed via trails, property boundaries, and stream corridors; roadsides and other areas adjacent to the refuge were included in the survey. Typically specimens were not collected unless flowers or fruits were present; telescoping tree pruners that could extend to about eight meters were used to reach accessible specimens from the lower canopy. Specimens from higher in the canopy were obtained through the use of weighted throwing ropes, as well as from fallen branches. Collecting efforts were ground-based; no tree climbing was attempted. If possible, specimens were collected in triplicate. Digital images were obtained both in the field and prior to pressing as staged shots with a black backdrop. Detailed field notes were taken on habit (tree, shrub, or vine), twig features (such as sap, stipules, odor), floral features (such as numbers of floral parts and colors, ovary position), and fruit features (color, odor, locules), as well as notes on habitat and GPS coordinates.

The plant drying method described by Blanco et al. (2006) was used; this method worked very well, usually drying the specimens in one to three days. The specimens were divided into three sets, with the primary set for the Herbario Nacional (CR), another set for Eastern Kentucky University (EKY), and a third set for Missouri Botanical Garden (MO). Duplicates of pteridophyte and bryophyte collections were designated for Morehead State University (MDKY).

Primary references used for the identification work were: 1) the Dendro-Matrix notebook prepared by RLJ, based on participation in the Tropical Dendrology course organized by HJS in 2001 (Jiménez-Saa, 1999); 2) Gentry (1993); 3) Hammel et al. (2003a, 2003b, 2004, 2007, 2010); 4) Weber et al. (2001); and 5) the four volume set on *Arboles de Costa Rica* (Holdridge et al. 1997, Zamora et al. 2000, 2004, 2011). Other useful references included Davidse et al. (1995), Krings and Braham (2005), Keller (2004), Mickel and Smith (2004), Zamora and Pennington (2001), and the popular books with color photographs by Zuchowski (2005) and Gargiullo et al. (2008). The listings and discussions of species at the site by Alexander Skutch in two of his books (Skutch 1980, 1992) were also helpful. A number of specialists in various plant groups were consulted (see Acknowledgements). Several internet sites also proved very helpful in identifying specimens, especially Neotropical Herbarium Specimens (2014), Smithsonian Tropical Institute Herbarium (2014), and INBio (2012).

Angiosperm family classification follows Stevens (2001 onwards), and author abbreviations follow IPNI (2014). Pteriodophyte family classification follows Smith et al. (2006). Binomial and trinomial nomenclature is based on The Plant List (2013). In the few cases when the name used in the *Manual de Plantes de Costa Rica* (Hammel et al. 2003b, 2004, 2007, 2010) differs from the accepted name in The Plant List, then that name is given in parenthesis. No species authorities are given for native or naturalized species mentioned in the text, as these are provided in Appendix 1. Authorities are included for non-native species discussed in the text but not listed in Appendix 1.

RESULTS

General Overview

A total of 314 species of woody plants and/or vines, belonging to 217 genera and 84 families was documented as part of the naturally occurring (native or naturalized) flora of Los Cusingos (Appendix 1). All but ten of the species records are based on specimens collected during this study; the additional ten records are based on Los Cusingos specimens already deposited by other collectors at CR. The total of 314 includes 298 native species and 16 non-native species. Families with ten or more species were: Melastomataceae (35 species), Fabaceae (30), Rubiaceae (20), Malvaceae (13), Solanaceae (11), Moraceae (10), and Sapindaceae (10). The genera with five or more species were: *Miconia* (14 species), *Psychotria* (10), *Piper* (6), *Clidemia* (5), *Ficus* (5), and *Inga* (5). Of the 314 total, only about 100 of the species were listed in the database obtained from the Herbario Nacional for Pérez Zeledón Canton.

Twenty-five species of pteridophytes and monocots were documented. There were three species of climbing or scrambling ferns and four species of arborescent ferns. For monocots there were eight species of palms, three species of cyclanths, and seven species of graminoids.

The following definitions were used to group the dicotyledonous species into major habit forms: a) vines are those species that climb or scramble on other vegetation; b) shrubs are those woody species that are multi-stemmed from the base and known to reach heights of less than 5 m (shrubby epiphytes and shrubby parasites are also distinguished); c) treelets are those woody species with a single main stem that are known to reach heights of 5 to 15 m; d) trees are those woody species with a single main stem that are known to reach heights of 15 to 30 m; and e) emergent trees are those woody species with a single main stem that are known to reach heights greater than 30 m. Of the 289 dicotyledonous species, 57 were classified as vines, 50 as terrestrial shrubs, 6 as epiphytic shrubs or cacti, 5 as parasitic shrubs, 154 as treelets or trees (species in Appendix 1 identified as "shrub or treelet," or "treelet or tree," are grouped in this category), and 17 as emergent trees.

Rare and Endemic Species

There are several sources of information on the status of threatened and endangered species in Costa Rica, including IUCN (2013), and the CITES and MINAE lists maintained at the INBio website, Species of Costa Rica (INBio 2007). The following species documented at Los Cusingos are included on at least one of these references, and are listed below with their threat category, source of listing, and number of sites at Los Cusingos:

1) *Cedrela odorata*, IUCN Vulnerable (Americas Regional Workshop 1998)—few sites in gardens and open areas.
2) *Cyathea bicrenata* (*trichiata*), Theatened or Reduced Populations (INBio 2007, CITES and MINAE)—two sites, near garden and along trail.
3) *Cyathea delgadii*, Threatened or Reduced Populations (INBio 2007, CITES and MINAE)—two sites along trail and near gardens.
4) *Cyathea multiflora*, Threatened or Reduced Populations (INBio 2007, CITES and MINAE)—many sites on trails
5) *Cecropia obtusifolia*, IUCN Least Concern, (Mitre 1998)—several sites on trails.
6) *Enterolobium schomburgkii,* UCN Least Concern, (Groom 2012)—one site in field
7) *Tabernaemontana* (*Stemmademia*) *pauli*, IUCN Vulnerable, (World Conservation Monitoring Centre 1998)—two sites on trails
8) *Swartzia costaricensis* (*simplex*), IUCN Least Concern, (López Poveda 2012)—one site along river.
9) *Tocoyena pittieri*, IUCN Vulnerable, (Nelson 1998)—one site along river
10) *Weberocereus imitans*, IUCN Endangered (Hammel 2013)—one site at forest edge near gardens.

Based on a database provided by the Herbario Nacional and on listings maintained by INBIo (2007), two of the above species are considered as endemics of Costa Rica—*Tabernaemontana pauli* and *Weberocereus imitans*. Other Costa Rica endemics at Los Cusingos include *Aphelandra golfoducensis*, *Costus stenophyllus* (planted), *Dendrophthora turrialbae*, *Eugenia grayumii*, and *Heliconia danielsiana*.

Non-native Species

Several non-native species were documented from the forested or disturbed regions of Los Cusingos, but none appeared to be particularly invasive. The following sixteen non-native species are either naturalized at Los Cusingos or have the potential to become naturalized [see Lobo Cabezas (2012) and Vargas (2009)] and are included in the species list in Appendix 1: *Acacia mangium*, *Anacardium occidentale*, *Antigonon leptopus*, *Bambusa vulgaris*, *Coffea arabica*, *Elaeis guineensis*, *Erythrina poeppigiana*, *Justicia betonica*, *Bryophyllum pinnatum*, *Manihot esculenta*, *Morus alba*, *Pyrostegia venusta*, *Stachytarpheta mutabilis*, *Spathodea campanulata*, *Theobroma cacao*, and *Syzygium jambos*.

The Pamela Lankester Garden

A botanical garden, named after Pamela Lankester, the wife of Alexander Skutch, has been developed around the homesite, and features many plants originally obtained by Skutch. Many of these plants were mentioned in his books, and he often commented on the types of birds attracted to the different species. These early plantings have been supplemented by additional species in recent years. Many of these are non-native, but some native species can also be found in the gardens. Lehman et al. (2009) prepared a guide (with color images and a map) for these gardens.

There was a variety of plant groups represented in the gardens. Large herbs and similar plants included species of *Alpinia, Calathea, Codiaeum, Cordyline, Costus, Etlingera, Hedychium, Heliconia,* and *Megaskepasma.* Fence-row plants included *Dracaena fragrans* (L.) Ker Gawl, *Gliricidia sepium,* and *Yucca guatemalensis* Baker. Hedge-row plants included *Ligustrum vulgare* L. and *Hibiscus rosa-sinensis* L., with *Arachis pintoi* Krapov & W.C. Greg. and *Impatiens walleriana* Hook.f. planted as a groundcover in some areas. *Bambusa vulgaris* formed a large thicket in the woodland edge behind the Skutch home. *Cycas revoluta* Thunb. has been planted, and was the only gymnosperm on the property. Many plants producing economically important fruits were present in the gardens, including *Annona muricata* L., *Artocarpus altilis* (Parkinson) Fosberg, *Averrhoa carambola* L., *Bactris gasipaes* Kunth, *Citrus* spp., *Coffea arabica* L., *Mangifera indica* L., *Musa* spp., *Persea americana* L., *Psidium guajava, Sambucus* spp., *Syzygium malaccense* (L.) Merr. & L.M.Perry, and *Theobroma cacao.* Other introduced species documented from the gardens and around the buildings, but not considered as part of the native or naturalized flora were: *Allamanda cathartica* L., *Arundina graminifolia* (D. Don) Hochr., *Ardisia elliptica* Thunb., *Azadirachta indica* A.Juss., *Crotalaria micans* Link, *Leea guineensis* G. Don, *Plumeria rubra* L., and *Thunbergia mysorensis* (Wight) T.Anderson. It should be noted that some of these non-native species have the potential to become invasive, especially *Alpinia* spp., *Arachis pintoi, Etlingera* spp., *Hedychium* spp., and *Impatiens walleriana.* The following native species were documented from the gardens: *Acnistus arborescens, Cecropia peltata, Cedrela odorata, Costus stenophyllus*, *Clusia croatii*, *Crescentia cujete, Ficus* spp., *Albizia saman*, and *Vochysia ferruginea.*

Native and Naturalized Plants of Los Cusingos

Pteridophytes

Three woody pteridophyte species with viny or vinelike habit, as well as four species of tree ferns, were documented. The viny species were *Gleichenella pectinata*, *Polybotrya caudata*, and *Salpichlaena volubilis*. The climbing *Salpichlaena* was exceedingly abundant and weedy, as Skutch had described in his writings (Skutch 1992). The species of *Polybotrya* lacked reproductive material, and the assigning of this fern to *P. caudata* is tentative—another possibility is *P. gomezii* R.C.Moran. It was common along the less disturbed sections of the trails through the primary forest and along streams, often found climbing on tree trunks. *Gleichenella pectinata* was observed only in one open, trail-side area near the researcher's cabin, where it formed a large colony scrambling over other vegetation. The tree ferns were *Alsophila firma, Cyathea bicrenata, C. delgadii,* and *C. multiflora*. The last-mentioned species was, by far, the most common tree fern with *C. delgadii* and *A. firma* patchily distributed within the refuge and *C. bicrenata* only observed as single individuals in two locations.

Additional work on the pteridophyte (as well as the bryophyte) flora has been initiated, but is yet incomplete. A few common and conspicuous species have been identified: *Pteridium aquilinum* (L.) Kunth formed a large population on the disturbed river bank in the southeastern section of the refuge; epiphytic ferns included

Microgramma lycopodioides (L.) Copeland, *Niphidium crassifolium* (L.) Lellinger, and *Serpocaulon triseriale* (Sw.) A.R. Sm. Preliminary observations and collections suggest that the Polypodiaceae and Hymenophyllaceae are particularly species-rich at Los Cusingos. Other families with several species observed at the study site were Blechnaceae, Dennstaedtiaceae, Lomariopsidaceae, and Selaginellaceae.

Palm and Palmlike Species (Arecaceae and Cyclanthaceae)

Palm and palmlike plants at Los Cusingos totalled 11 species, and including several tree-sized and dwarf palms. The most conspicuous and abundant of the tall palms was *Socratea exorrhiza*, notable for its widely spaced and spiny prop roots. Another tall palm was the palmito, *Euterpe precatoria*, with the prop roots densely packed and nearly smooth. Several dwarf palms and palmlike species occur in the understory, including two species of *Bactris*, two species of *Geonoma*, and one species of *Chamaedorea*. Three species in the palmlike Cyclanthaceae were documented: *Asplundia alata*, *A. euryspatha,* and *Carludovica drudei*.

Woody and Climbing Graminoids (Cyperaceae and Poaceae)

Seven woody or climbing grasses and sedges were documented at Los Cusingos. These include two kinds of bamboo, the non-native *Bambusa vulgaris* and the native *Chusquea simpliciflora*. A semi-woody grass, *Lasiacis procerrima,* reaching over 3 m in height, dominated large openings on lower terraces near the river. Three species of climbing grasses were documented, *Lasiacis rugelii*, *L. sorghoidea*, and *Olyra latifolia*. These species often climb into the lower branches along the trails and dangle from branches. A prickly sedge, *Scleria secans*, was also abundant, dangling from branches and posing an entangling hazard for hikers.

Other observations on the monocot flora at Los Cusingos

A rich monocot flora exists at Los Cusingos, with the families Araceae, Bromeliaceae, and Orchidaceae appearing to be particularly species-rich. These non-woody groups were not targeted during this study, but many were photographed, and some were documented with collections. The following taxa were noted at Los Cusingos: Araceae—*Anthurium* spp., *Dieffenbachia* spp., *Dracontium* spp., *Monstera deliciosa* Liebm., and *Philodendron* spp.; Costaceae—*Costus guanaiensis* Rusby, *Costus scaber* Ruiz & Pavon; and *Costus stenophyllus* Standl. & L.O. Williams; Heliconiaceae—*Heliconia danielsiana* W.J. Kress, *Heliconia irrasa* Lane ex R.R. Sm., and other *Heliconia* spp.; Marantaceae—*Calathea* spp.; and Orchidaceae—*Brassia gireoudiana* Rchb.f. & Warsz., *Epidendrum* spp., *Gongora* spp., *Oncidium* spp., and *Xylobium* spp. Many of these taxa can be found in and around the gardens at Los Cusingos, either occurring naturally or having been transplanted from the surrounding forest.

Epiphytic and Parasitic Shrubs

Five species of woody parasites were documented, in two families: Loranthaceae—*Psittacanthus schiedeanus*, *Struthanthus leptostachyus*, and *S. orbicularis*; and in the Santalaceae—*Dendrophthora turrialbae* and *Phoradendron crassifolium*. The *Psittacanthus* formed red and yellow patches at the tops of some trees near the researcher's cabin, and the other species were found in lower to upper branches of trees along the forest edges or in open fields.

Six shrubby epiphytes in five families were documented, and these included two with dangling branches: the red/white-flowered *Satyria panurensis*, and the orange-flowered *Juanulloa mexicana*, and two with more upright habit, the white/orange-flowered *Drymonia macrantha* and white/red flowered *Souroubea vallicola*. At least two species of epiphytic cacti occur in the area: *Epiphyllum phyllanthus* and the endangered *Weberocereus imitans*.

The epiphytic and parasitic flora at Los Cusingos is obviously much richer than indicated by the documentation of the 11 shrubby taxa listed above. Many tree or treelet species, especially in such genera as *Clusia* and *Ficus*, often initiate their growth as epiphytes. Because they reach greater sizes than the shrubby species above, they are categorized as treelets or trees for the purposes of this report.

Climbing Dicotyledonous species

The dicotyledenous vine flora is particularly rich at Los Cusingos, with 57 species documented in 20 families. There were seven species in the Sapindaceae, six species in the Fabaceae, five species in the Bignoniaceae, and four each in the Apocynaceae, Menispermaceae, Passifloraceae, and Vitaceae. Other families with numbers of viny species indicated parenthetically include the following: Acanthaceae (2), Aristolochiaceae (1), Asteraceae (2), Campanulaceae (1), Cucurbitaceae (2), Dilleniaceae (1), Loganiaceae (2), Malphigiaceae (2), Melastomataceae (1), Polygalaceae (1), Polygonaceae (1), Rhamnaceae (2), and Schlegeliaceae (1). *Davilla kunthii* in the Dilleniaceae was very common, as were *Entada gigas* and *Mucuna holtonii* in the Fabaceae. *Macroscepis hirsuta* (Apocynaceae) and *Schlegelia parviflora* (Schlegeliaceae) were rare. Introduced vines included *Antigonon leptopus* and *Pyrostegia venusta*.

Shrubs

There were 50 species of terrestrial shrubs documented, with the major families and number of species as follows: Melastomataceae (11), Rubiaceae (9), Solanaceae (9), and Asteraceae (4). All of the 9 shrub species in the Rubiaceae were in the genus *Psychotria*, and there were 4 shrubby species in the genus *Clidemia* (Melastomaceae). The endemic *Aphelandra golfodulcensis* was found at only a single site. *Poikilacanthus macranthus* was common along trails in the forest understory. *Psychotria elata* and *P. poeppigiana*, the famous "hot lips" plants, were also very common, especially in more open places.

Treelets and Trees

There were 154 species classified as treelets or trees (woody plants commonly reaching heights of 5 to 30 m). These species comprised almost half of the woody species at Los Cusingos. Families with five or more species of treelets or trees are as follows, all except Rubiaceae with a majority of their species in this category: Clusiaceae (5/6), Euphorbiaceae (6/7), Fabaceae (17/25), Lauraceae (5/6), Melastomaceae (21/33), Moraceae (8/9), Myrtaceae (5/5), Piperaceae (6/6), and Rubiaceae (8/18). Several of the tree species are non-native and naturalized in the area, including *Acacia mangium*, *Erythrina poeppigiana*, and *Syzygium jambos*. Genera with the largest number of species in this category were *Miconia* (13 species), *Piper* (6), *Ficus* (5), *Inga* (5), and *Psychotria* (5). See the Discussion for further listings of these tree and treelet species associated with various habitats at Los Cusingos.

Emergent Trees

Seventeen emergent species were identified, these being the trees capable of reaching the greatest heights and with crowns projecting above the canopy formed by the majority of the trees. Two of the largest individuals in diameter were a *Brosimum utile* along Quebrada Cusingos, and a *Ceiba pentandra* along the Rio Peñas Blancas, north of the Toma de Agua, at the convergence of the two streams. Both trees were about 140 cm dbh. There were numerous other trees close to 100 cm dbh. The following is a list of emergent species at Los Cusingos: *Brosimum utile*, *Buchenavia tetraphylla*, *Ceiba pentandra*, *Dilodendron costaricense*, *Ficus tonduzii*, *Humiriastrum diguense*, *Lafoensia punicifolia*, *Ocotea cernua*, *Pourouma bicolor*, *Pouteria torta* subsp. *tuberculata*, *Sloanea laurifolia*, *Sterculia recordiana*, *Symphonia globulifera*, *Terminalia oblonga*, *Virola surinamensis*, *Vochysia ferruginea*, and *V. guatemalensis*.

DISCUSSION

This study has resulted in a substantial increase in the number of herbarium specimens from this northern section of the Río General valley. Prior to this study only about 30 woody and/or viny species had been recorded from Los Cusingos; 314 have now been documented at Los Cusingos, and only about 100 of these species were listed in databases provided by the Herbario Nacional for Pérez Zeledón Canton. These collections also provided additional records for species and genera with only a few representative specimens in the Herbario Nacional, as well as additional flowering and fruiting specimens of the less collected (and difficult to press) species in the Arecaceae and other large-leaved groups. Several of the species documented were listed by Hammel et al. (2004) as indicative of remnant populations in the Río General valley of species more typical of the Osa Peninsula, including the following: *Annona amazonica, Brosimum utile, Buchenavia tetraphylla, Gouania colombiana, Humiriastrum diguense, Sloanea laurifolia, Socratea exorrhiza,* and *Virola surinamensis*.

As described in Hartshorn (1983), a typical mature forest community of the Tropical Premontane Wet Forest life zone is a medium to tall, semi-evergreen forest with two or three strata. The canopy trees are 30 to

40 m tall, frequently covered by a dense layer of moss, and often buttressed. The understory trees are 10 to 20 m tall with deep crowns, including palms with stilt roots and occasional tree ferns. A dense shrub layer 2 to 3 m tall is also often present. The ground layer in this forest type is composed mostly of ferns, with epiphytes being present but not conspicuous, and with abundant climbing vines. This description generally fits the forested sites at Los Cusingos.

A typical site within the relatively undisturbed forest community at Los Cusingos would include emergent species, some with extensive buttresses, such as *Brosimum utile*, *Ceiba pentandra*, *Ficus tonduzii*, *Humiriastrum diguense*, *Lafoensia punicifolia*, *Mouriri gleasoniana*, *Sloanea laurifolia*, *Symphonia globulifera*, *Virola surinamensis*, *Vochysia ferruginea*, and *V. guatemalensis*. The understory of trees, treelets, and shrubs included many kinds of dicotyledonous trees, with *Myrciaria floribunda, Tovomita weddeliana*, and *Vismia macrophylla* being common. Other species in the understory included at least two species of tall palms with stilt roots (*Socratea exorrhiza*, very common, and *Euterpe precatoria*, less common), with several species of shrubby palms (species of *Bactris*, *Chamaedorea*, and *Geonoma*) being abundant as well. Tree ferns were also present and mostly under five meters tall, with *Alsophila firma* and *Cyathea multiflora* most common. High-climbing vines, especially *Entada gigas* and *Mucuna holtonii,* were conspicuous, and *Salpichlaena volubilis* was nearly ubiquitous. Thick layers of moss were present on the tree trunks and branches, and epiphytes were common.

Tree species that tended to be more common in secondary forests and other areas of recent disturbance include *Alchornea latifolia, Bellucia pentamera, Byrsonima crassifolia, Cecropia peltata, Cedrela odorata, Clusia* spp., *Cordia bicolor, Dendropanax arboreus, Erythrina* spp., *Gliricidia sepium, Goelthalsia meiantha, Guatteria recurvisepala, Heliocarpus americanus, Inga* spp., *Jacaranda copaia, Maquira guianensis, Miconia* spp. (and other genera and species in the Melastomataceae), *Piptocoma discolor, Pourouma bicolor, Protium* spp., *Schefflera morototoni, Simarouba amara, Stryphnodendron microstachyum, Turpinia occidentalis,* and *Vismia* spp.

Zygia longifolia was probably the most important canopy tree along the major river corridor; *Ficus* spp. and *Dendropanax arboreus* were also common. Other species noted predominantly along the Rio Peñas Blancas and the smaller streams included: *Condaminea corymbosa, Marila laxiflora*, *Protium tenuifolium*, *Sorocea affinis*, *Swartzia costaricensis*, *Tetragastris panamensis*, and the rare *Tocoyena pittieri*.

Of the tree species mentioned by Skutch (1980, 1992) several were not observed during this study, in particular the campana tree (*Gordonia fruticosa*), and the ira chiricano (*Vantanea barbourii*). Skutch had noted that the campana trees seemed to be dying out, and replaced by *Brosimum utile*. The ira chiricano was also searched for, but only its close relative, *Humiriastrum diguense*, also called chiricano, was located. It should be noted that specimens could not be obtained from some tall trees at Los Cusingos, and their identity remains unknown.

Studies of other mid-elevation sites in Costa Rica (Fournier et al. 1985; Wattenberg & Breckle 1995; Homeier et al. 2005; Cascante Marín et al. 2012) reported forest compositions very different from that of Los Cusingos. Most of the prominent species at Los Cusingos were not present at these other sites. Some sites reported by Holdridge et al. (1971) as Tropical Premontane Wet were generally similar to the Los Cusingos forest. A site near San Isidro de El General at 620 meters elevation shared many species with Los Cusingos, including *Brosimum utile*, *Dendropanax arboreus*, *Sloanea laurifolia*, *Socratea exorhizza*, *Symphonia globulifera*, and about a dozen other species in common with Los Cusingos. Several other premontane wet sites were described but all had very few species in common with those of Los Cusingos.

As noted by Hammel et al. (2004), such forest fragments as represented by Los Cusingos provide a glimpse into the past, a suggestion of the types of forest communities that once covered this great river valley. From a Google Earth view, Los Cusingos and a few nearby forested (but unprotected) tracts stand out in an otherwise significantly altered landscape that extends northwest about 5 km to the lowermost forested ridges of Cerro Chirripó. Hardly any other substantial forest tracts can be seen for some 15 km southeast—the entire valley between Cerro Chirripó and the Fila Costena (Coastal Mountain Range) has essentially been deforested. Such a view magnifies the significance of Los Cusingos, as it is currently the largest protected tract in an area of about 35 sq km southwest of Chirripó National Park and northeast of Hermosa and Peñas Blancas. This rectangular region immediately south of Cerro Chirripó has now been designated by the Tropical Science Center as the Alexander Skutch Biological Corridor; this corridor will link the remaining forest patches in the vicinity with the extensive forests occupying the steep ridges extending south from Chirripó National Park. Los Cusingos has become a focal point of work to develop this wildlife corridor project and to establish working relationships with the local people to encourage their assistance in protecting the remaining resources of the area.

Although widely known as a bird sanctuary, Los Cusingos can also be considered as a remnant biological community, providing a haven for the many kinds of life associated with the long-vanished forests of the Río General valley. The refuge can thus serve as a living laboratory for a variety of studies on the plants, animals, and their interactions, and provide a better understanding of what has happened to these ecosystems in the past, and what may happen in the future.

In his *A Naturalist in Costa Rica* (1992), Skutch provides some vivid descriptions of what the countryside was like, and what came to be. When he first entered the Río General valley in 1935 there were "vast areas of forest untouched by the ax, stretching in unbroken majesty from the seacoast to the open paramos of the Cordillera de Talamanca." He later observed that the "destructions of the forests … has been particularly striking in this valley … of the once magnificent wilderness only shreds and patches remain in the valley … one of the largest remaining tracts of forest in the valley is that of a 100 acres of so on this farm, which for nearly thirty years I have tried to preserve in its pristine state." He lived for 63 years at Los Cusingos, simply and close to the earth. He witnessed the loss of the surrounding forests, but he continued to protect his land, and to study, and to write: "And of the things that have gone, some have been preserved, albeit imperfectly, in memory and in writings, in which I have tried to convey to others their interest and beauty."

APPENDIX 1

Native and naturalized vascular plant species of Los Cusingos. Collection numbers for specimens collected by RLJ and HJS are listed without initials; ACR refers to specimens collected by ACR, RLJ, and HJS. Other specimens from Los Cusingos already housed at CR are indicated by collector name and collection number. Non-native species are indicated by an asterisk (*). See text for definitions of habit forms.

I. PTERIDOPHYTES—woody and/or climbing ferns

Blechnaceae

Salpichlaena volubilis (Kaulf.) J. Sm. 10,136; ACR 17,418; climbing fern.

Cyatheaceae

Alsophila firma (Baker) D.S. Conant. 10,556; ACR 17,530, 17,585; arborescent fern.
Cyathea bicrenata Liebm. ACR 17424, 17,555; arborescent fern.
Cyathea delgadii Sternb. ACR 17,529, 17, 586; arborescent fern.
Cyathea multiflora Sm. 10,242; ACR 17,419, 17,440, 17,587; arborescent fern.

Dryopteridaceae

Polybotrya caudata Kunze. 9886, 10,240; ACR 17,453; climbing fern.

Gleicheniaceae

Gleichenella pectinata (Willd.) Ching 9868; ACR 17574; scrambling fern.

II. ANGIOSPERMS—woody and/or climbing monocots

Arecaceae

Bactris glandulosa Oerst. 10,180; shrubby palm.
Bactris hondurensis Standl. 10,150; ACR 17,532; shrubby palm.
Chamaedorea tepejilote Liebm. 10,204; shrubby palm.
Elaeis guineensis Jacq. 10,149; arborescent palm.
Euterpe precatoria Mart. 10,151, 10166, 10212; arborescent palm.
Geonoma ferruginea H. Wendl. ex Spruce. 10,029; shrubby palm.
Geonoma pinnatifrons Willd. subsp. *oxycarpa* (Mart.) A.J. Hend. 10,213; shrubby palm.
Socratea exorrhiza (Mart.) H. Wendl.10, 251; arborescent palm.

Cyclanthaceae

Asplundia alata Harling. 10,224; shrubby cyclanth.
Asplundia euryspatha Harling. 10,162; climbing cyclanth.
Carludovica drudei Mast. 10,181; shrubby cyclanth.

Cyperaceae

Scleria secans (L.) Urb. 10,099; prickly climbing sedge.

Poaceae

**Bambusa vulgaris* Schrad. 10,066; non-native bamboo.
Chusquea simpliciflora Munro. 10,370; native bamboo.
Lasiacis maculata (Aubl.) Urb. [=*L. sorghoidea* (Ham.) Hitchc. & Chase]. 10,131; climbing grass.
Lasiacis procerrima (Hack.) Hitchc. 9856. semi-woody grass.
Lasiacis rugelii (Griseb.) Hitchc. 9940; climbing grass.
Olyra latifolia L. 10,036, 10,154; bamboo-like grass.

III. ANGIOSPERMS—woody and/or climbing dicots

Acanthaceae

Aphelandra golfodulcensis McDade. 9950; shrub.
**Justicia betonica* L. 9817; shrub.
Mendoncia gracilis Turrill. 10,207; woody vine.
Mendoncia lindavii Rusby. 10,390; woody vine.
Odontonema tubaeforme (Bertol.) Kuntze. 10,047, 10197; shrub.
Poikilacanthus macranthus Lindau. 9841; shrub.

Thunbergia erecta (Benth.) T. Anderson. 9961, 10,031; woody vine.

Achariaceae
Lindackeria laurina C. Presl. 9878, 9921, 10,534; shrub or treelet.

Actinidiaceae
Saurauia montana Seem. 10,394; tree.

Anacardiaceae
*Anacardium occidentale L. 9939; tree.
Spondias radlkoferi Donn. Sm. 10,210; tree.

Annonaceae
Annona amazonica R.E.Fr. Q. Jiménez 1591 (CR); tree.
Guatteria recurvisepala R.E. Fr. 9823, 9884; tree.
Xylopia frutescens Aubl. 10,248; treelet.

Apocynaceae

Macroscepis hirsuta (Vahl) Schltr. 10,133; woody vine.
Mandevilla hirsuta (Rich.) K.Schum. 9844, 9901; woody vine.
Peltastes isthmicus Woodson. 9946; woody vine.
Prestonia portobellensis (Beurl.) Woodson. 10,100; woody vine.
Tabernaemontana donnell-smithii Rose ex J.D. Sm. 10,205; tree.
Tabernaemontana pauli (Leeuwenb.) A.O. Simões & M.E. Endress. 10,155, 10,165; tree.

Araliaceae
Dendropanax arboreus (L.) Decne. & Planch. 9888, 9962, 9987; tree.
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin. 10,008, 10085; tree.

Aristolochiaceae
Aristolochia pilosa Kunth. 10,057; herbaceous vine

Asteraceae
Eirmocephala brachiata H. Rob. 10,032; shrub.
Hidalgoa ternata La Llave. 10,178; woody vine.
Lasianthaea fruticosa (L.) K.M. Becker. 9827; shrub.
Mikania riparia Greenm. ex B.L. Rob. 9829. Semi-woody vine.
Piptocarpha poeppigiana (DC.) Baker. 10,079; shrub.
Piptocoma discolor (Kunth) Pruski. 9885; tree.
Zexmenia virgulta Klatt. 9857; shrub.

Begoniaceae
Begonia multinervia Liebm. 9965, 10,033; shrubby begonia.

Bignoniaceae
Callichlamys latifolia (Rich.) K. Schum. 10,164; woody vine.
Crescentia cujete L. 10,065; treelet.
Fridericia patellifera (Schltdl.) L.G. Lohman. 9914; woody vine.
Handroanthus ochraceus (Cham.) Mattos. 10,157; tree.
Jacaranda copaia (Aubl.) D. Don. 10,148; tree.
Lundia corymbifera (Vahl) Sandwith. 10,536; woody vine.
Pleonotoma variabilis (Jacq.) Miers. 9873; woody vine.
**Pyrostegia venusta* (Ker Gawl.) Miers. 9990; woody vine.
**Spathodea campanulata* P. Beauv. 10,123; tree.

Bixaceae
Bixa orellana L. 9947; tree.

Boraginaceae
Cordia bicolor A. DC. 10,161; tree.
Cordia curassavica (Jacq.) Roem. & Schult. 9974; shrub.
Tournefortia bicolor Sw. 10,101; shrub.

Burseraceae
Protium ravenii D.M. Porter. 10,092, 10,363, 9830; tree.
Protium tenuifolium (Engl.) Engl. subsp. *sessiliflorum* (Rose) D.M. Porter. 10,027, 10,374b; tree.
Tetragastris panamensis (Engl.) Kuntze. 10374a; tree.

Cactaceae
Epiphyllum phyllanthus (L.) Haw. 10,082; epiphytic cactus.
Weberocereus imitans (Kimnach & Hutchinson) Buxb. 10,194; epiphytic cactus.

Calophyllaceae
Marila laxiflora Rusby. 10,078, 9942; tree.

Campanulaceae
Centropogon granulosus C. Presl. 10,392; woody vine.

Cannabaceae
Celtis iguanaea (Jacq.) Sarg. 10,114, 10,217; shrub or treelet.
Trema micrantha (L.) Blume. 10,116; shrub or treelet.

Caricaceae
Jacaratia dolichaula (Donn. Sm.) Woodson. 9840; tree.

Chysobalanaceae
Licania platypus (Hemsl.) Fritsch. 10,062, 10159; tree.

Clethraceae
Clethra lanata M. Martens & Galleotii. (*C. costaricensis* Britton). 10,107; D. Norby 365 (CR); tree.

Clusiaceae
Chrysochlamys glauca (Oerst., Planch., & Triana) Hemsl. 9983; shrub or treelet.
Clusia croatii D'Arcy. 9955, 10,045, 10,063, 10189; shrub or treelet, usually epiphytic.
Clusia uvitana Pittier. 10,211; shrub or treelet, sometimes epiphytic.
Garcinia intermedia (Pittier) Hammel. 9988; treelet or tree.
Symphonia globulifera L.f. 9943, 10,090; emergent tree.
Tovomita weddeliana Planch. & Triana. 9903; shrub or treelet.

Combretaceae
Buchenavia tetraphylla (Aubl.) R.A. Howard. 10,080; emergent tree
Terminalia oblonga (Ruiz & Pav.) Steud. 10,097; emergent tree.

Convolvulaceae
Jacquemontia ciliata Sandwith. 9815; herbaceous vine.
Maripa nicaraguensis Hemsl. 10,004, 10,049, 10,176, 10,537; woody vine.

Crassulaceae
**Bryophyllum pinnatum* (Lam.) Oken. [=*Kalanchoe pinnata* (Lam.) Pers.]. 9944; shrub.

Cucurbitaceae
Gurania coccinea Cogn. 9899, 9915; woody vine.
Sechium pittieri (Cogn.) C. Jeffrey. 9995; woody vine.

Dichapetalaceae
Dichapetalum brenesii Standl. 9999; shrub or treelet.

Dilleniaceae
Davilla kunthii A.St.-Hil. 9863, 9898; woody vine.

Elaeocarpaceae
Sloanea laurifolia (Benth.) Benth. 10,172, 10019; emergent tree.

Ericaceae
Satyria panurensis (Benth. ex Meisn.) Hook.f. ex Nied. 10,127; epiphytic shrub.

Erythroxylaceae
Erythroxylum citrifolium A. St.-Hil. 10,042; shrub or treelet.
Erythroxylum macrophyllum Cav. 10,025; shrub or treelet.

Euphorbiaceae
Acalypha diversifolia Jacq. 10,104; shrub or treelet.
Acalypha macrostachya Jacq. 9864; shrub or treelet.
Alchornea latifolia Sw. 9836, 9929, 9948; tree.
Croton draco Schltdl. 9985, 10,401; treelet or tree.

Croton smithianus Croizat. 10,028, 10371, 10043, 10220; treelet or tree.
Croton tenuicaudatus Lundell. 9934, 10,022; treelet or tree.
**Manihot esculenta* Crantz. 9941; shrub.

Fabaceae

**Acacia mangium* Willd. 10,198; tree.
Albizia saman (Jacq.) Merr. 10,560; tree.
Calliandra calothyrsus Meisn. 10,000; shrub or treelet.
Calliandra riparia Pittier. 9871; shrub or treelet.
Canavalia brasiliensis Mart. ex Benth. 9860; woody vine.
Diphysa americana (Mill.) M. Sousa. 10,076; shrub or treelet.
Entada gigas (L.) Fawc. & Rendle. 9838; woody vine.
Enterolobium schomburgkii (Benth.) Benth. 9930; tree.
Erythrina costaricensis Micheli. 10,017; shrub or treelet.
Erythrina fusca Lour. 10,002; tree.
**Erythrina poeppigiana* (Walp.) O.F. Cook. 9913, 10,001; tree.
Gliricidia sepium (Jacq.) Kunth ex Walp. 9892, 10109; treelet or tree.
Inga edulis Mart. 10,228; tree.
Inga oerstediana Benth. 10,106; tree.
Inga spectabilis (Vahl) Willd. 10,229 ; tree.
Inga thibaudiana DC. 9920, 9945; tree.
Inga umbellifera (Vahl) Steud. 9820, 9994; tree.
Machaerium kegelii Meisn. 10,115; woody vine.
Machaerium seemannii Benth. ex Seem. 9993, 9822; woody vine.
Mimosa myriadena (Benth.) Benth. 9923; woody vine.
Mucuna holtonii (Kuntze) Moldenke. 9874, 10,056; woody vine.
Platymiscium pinnatum (Jacq.) Dugand. 10,040; tree.
Senna hayesiana (Britton & Rose) H.S. Irwin & Barneby. 9821, 9971, 10,538; treelet or tree.
Senna spectabilis (DC.) H.S.Irwin & Barneby. 9839, 9991; treelet or tree.
Stryphnodendron microstachyum Poepp. 10052, 10,158; tree.
Swartzia costaricensis (Britton) N. Zamora. 9952; treelet or tree.
Zygia longifolia (Humb & Bonpl. ex Willd.) Britton & Rose. 9954, 10,369; tree.

Gesneriaceae

Drymonia macrantha (Donn. Sm.) D.N. Gibson. 10,072, 10,135; epiphytic shrub.

Humiriaceae

Humiriastrum diguense (Cuatrec.) Cuatrec. ACR 17,533; emergent tree.

Hypericaceae

Vismia baccifera (L.) Planch. & Triana. 10,026, 9870; tree.
Vismia macrophylla Kunth. 10,102; treelet.

Lacistemataceae

Lacistema aggregatum (P.J. Bergius) Rusby. 10,050, 10,119; shrub or treelet.

Lamiaceae

Cornutia pyramidata L. 10,054; shrub or treelet.
Scutellaria costaricana H. Wendl. 10,126; shrub.

Lauraceae

Beilschmiedia tovarensis (Klotzsch & H. Karst ex Meisn.) Sach. Nishida. 10,005a; tree.
Nectandra membranacea (Sw.) Griseb. 9968; tree.
Ocotea cernua (Nees) Mez. 9891; emergent tree.
Ocotea laetevirens Standl. & Steyerm. 9959. tree
Persea caerulea (Ruiz. & Pav.) Mez. 10,024; tree.

Loganiaceae

Strychnos chlorantha Progel. 10,223; woody vine.
Strychnos panamensis Seem. 9949; woody vine.

Loranthaceae

Psittacanthus schiedeanus (Schltdl. & Cham.) G. Don. 10,069; parasitic shrub.
Struthanthus leptostachyus (Kunth) G. Don 10,061; parasitic shrub.
Struthanthus orbicularis (Kunth) Eichler. 10,014, 9910; parasitic shrub.

Lythraceae

Lafoensia punicifolia DC. 10,111, 10,359; emergent tree.

Malphigiaceae

Banisteriopsis muricata (Cav.) Cuatrec. 10,232; woody vine.
Byrsonima crassifolia (L.) Kunth. 10,089; tree.
Stigmaphyllon puberum (Rich.) A. Juss. 9963, 9970; woody vine.

Malvaceae

Abutilon purpusii Standl. 9992; shrub or treelet.
Ceiba pentandra (L.) Gaertn. 10,252; emergent tree.
Goethalsia meiantha (Donn. Sm.) Burret. 10,039; tree.
Heliocarpus americanus L. 9861, 10169; tree.
Hibiscus furcellatus Lam. 9843; shrub.
Malvaviscus penduliflorus Moc. & Sessé ex DC. 10,122; shrub.
Pachira aquatica Aubl. 10,558; tree.
Pachira sessilis Benth. 10,367; tree.
Pavonia dasypetala Turcz. 10,016; shrub or treelet.
Pseudobombax septenatum (Jacq.) Dugand. 10,353; tree.
Sida urens L. 9866; shrub.
Sterculia recordiana Standl. 10,399; emergent tree.
**Theobroma cacao* L. 10,190; treelet.
Wissadula excelsior (Cav.) C. Presl. 9847; shrub.

Marcgravaceae

Souroubea vallicola Woodson ex de Roon. 10,058; epiphytic shrub.

Melastomataceae

Aciotis indecora (Bonpl.) Triana. 9849; shrub.
Adelobotrys adscendens (Sw.) Triana. 9826; woody vine.
Bellucia pentamera Naudin. 9889; treelet.
Blakea gracilis Hemsl. 9953. 10,175; shrub, sometimes epiphytic.
Clidemia capitellata (Bonpl.) D. Don. 9912; shrub.
Clidemia dentata Pav. ex D. Don. 10,006; shrub.
Clidemia discolor (Triana) Cogn. 0,117,10,173, 9852; shrub.
Clidemia hirta (L.) D. Don. 10,083; shrub.
Clidemia sericea D. Don. 10,095; shrub.
Conostegia subcrustulata (Beurl.) Triana. 10,202; shrub.
Conostegia superba D. Don ex Naudin. 10,219; shrub or treelet.
Graffenrieda galeottii (Naudin) L.O. Williams. 10,130; treelet.
Henriettea succosa (Aubl.) DC. 10,108; shrub or treelet.
Henriettella fascicularis (Sw.) C. Wright. 10,067; shrub or treelet.
Leandra grandifolia Cogn. 10,357, 10,364; shrub.
Miconia affinis DC. 10,064; shrub or treelet.
Miconia argentea (Sw.) DC. 9919; shrub or treelet.
Miconia bubalina Naudin. 10,146; shrub or treelet.
Miconia chrysophylla (Rich.) Urb. 9980, 10,139; treelet or tree.
Miconia elata (Sw.) DC. 9835; tree.
Miconia gracilis Triana. 9853, 10,177, 10,351; shrub or treelet.
Miconia holosericea (L.) DC. 10,233; shrub or treelet.
Miconia lacera (Bonpl.) Naudin. 10,391, 10,015, 10,535; shrub.
Miconia matthaei Naudin. 9834, 9848; shrub or treelet.
Miconia minutiflora (Bonpl.) DC. 10,554, 10,187; shrub or treelet.
Miconia prasina (Sw.) DC. 10,218; shrub or treelet.
Miconia schlimii Triana. 10,129, 10,203; shrub or treelet.
Miconia serrulata (DC.) Naudin. 9904; shrub or treelet.
Miconia trinervia (Sw.) D. Don ex Loudon. 9828, 10,010; tree.
Mouriri gleasoniana Standl. 9931, ACR 17,487; tree.
Ossaea macrophylla (Benth.) Cogn. 10,397; shrub or treelet.
Tibouchina longifolia (Vahl) Baill. D. Norby. 108 (CR); shrub.

Topobea maurofernandeziana Cogn. 9894; treelet.

Meliaceae
Cedrela odorata L. 10,055; tree.
Trichilia pallida Sw. S. Darwin 412 (CR); tree.

Menispermaceae
Abuta panamensis (Standl.) Krukoff & Barneby. 10,366; woody vine.
Cissampelos fasciculata Benth. 10,113; woody vine.
Cissampelos pareira L. 10,087; woody vine.
Odontocarya truncata Standl. 10,011; woody vine.

Monimiaceae
Mollinedia viridiflora Tul. 10,170; shrub or treelet.

Moraceae
Brosimum guianense (Aubl.) Huber ex Ducke. 10168; tree.
Brosimum utile (Kunth) Oken. 10,093, 10,138; emergent tree.
Ficus brevibracteata W.C. Burger. 10,244; tree, often epiphytic.
Ficus citrifolia Mill. 10,188; treelet, often epiphytic.
Ficus colubrinae Standl. 9957; treelet, often epiphytic.
Ficus costaricana (Liebm.) Miq. 10,243, 10,245, 9986; treelet, often epiphytic.
Ficus tonduzii Standl. 9960; emergent tree.
Maquira guianensis Aubl. 10,231, 10,199, 9938; tree.
**Morus alba* L. 10,227; treelet.
Sorocea trophoides W.C. Burger. 10,112; shrub or treelet.

Myristicaceae
Compsoneura excelsa A.C. Smith. 9837; tree.
Virola sebifera Aubl. 9833, 10532; tree.
Virola surinamensis (Rol. ex Rottb.) Warb. 10,132; ACR 17,492; emergent tree.

Myrtaceae
Eugenia grayumii Barrie. 9980; treelet.
Myrcia splendens (Sw.) DC. 10,247; treelet or tree.
Myrciaria floribunda (H. West ex Willd.) O.Berg. 10,091, 10,341, 9881; treelet or tree.
Psidium guajava L. 9989; treelet.
**Syzygium jambos* (L.) Alston. 10,023; treelet.

Nyctaginaceae
Neea laetevirens Standl. 10,018; shrub or treelet.
Neea psychotrioides Donn. Sm. 9922; shrub or treelet.

Passifloraceae
Passiflora ambigua Hemsl. 9858, 10,153; woody vine.
Passiflora costaricensis Killip. 10,361; herbaceous or woody vine.
Passiflora quadrangularis L. 9879; woody vine.
Passiflora vitifolia Kunth. 9875; woody vine.

Phytolaccaceae
Phytolacca rivinoides Kunth & C.D. Bouché. 9846; shrub.

Piperaceae
Piper aduncum L. 9997; shrub or treelet.
Piper arboreum Aubl. 9832, 10,005b; shrub or treelet.
Piper auritum Kunth. 9998; shrub or treelet.
Piper biseriatum C.DC. 10,209, 9845; shrub or treelet.
Piper corrugatum Kuntze. 10,137; Burger 4821 (CR); shrub or treelet.
Piper curtispicum C.DC. 10,365, 10,182; shrub or treelet.

Polygalaceae
Securidaca diversifolia (L.) S.F. Blake. 10,044; woody vine.

Polygonaceae
**Antigonon leptopus* Hook. & Arn. 9979; woody vine.

Primulaceae
Ardisia opegrapha Oerst. subsp. *wagneri* (Mez) Pipoly & Ricketson. 10,215; shrub or treelet.
Ardisia guianensis (Aubl.) Mez. 9982; shrub or treelet.

Rhamnaceae
Gouania colombiana Suess. 10,160; woody vine.
Gouania lupuloides (L.) Urb. 9906; woody vine.

Rubiaceae
**Coffea arabica* L. 10,530; shrub.
Condaminea corymbosa (Ruiz & Pav.) DC. 9981; treelet.
Hamelia patens Jacq. 10,355, 10,038; treelet.
Palicourea guianensis Aubl. 10,553; treelet.
Palicourea triphylla DC. 10,084; treelet.
Palicourea tetragona (Donn. Sm.) C.M. Taylor. 10,360; treelet
Psychotria aurantibractea C.M. Taylor. 10,221; shrub.
Psychotria berteroana DC. 10,238; treelet.
Psychotria deflexa DC. 10,346; shrub.
Psychotria elata (Sw.) Hammel. 9877; treelet.
Psychotria gracilenta Müll.Arg. 9854, 10140; shrub.
Psychotria marginata Sw. 9851; shrub.
Psychotria microbotrys Ruiz ex Standl. 10,171, 10,222; shrub.
Psychotria poeppigiana Müll.Arg. 9869; shrub.
Psychotria racemosa Rich. 10,009; shrub.
Psychotria solitudinum Standl. 9905; shrub.
Rudgea cornifolia (Kunth) Standl. D. Norby 452 (CR); treelet.
Sabicea panamensis Wernham. 10,020; woody vine.
Tocoyena pittieri (Standl.) Standl. 10,105; treelet.

Salicaceae
Banara guianensis Aubl. 10,021; shrub or treelet.
Casearia sylvestris Sw. 9819; shrub or treelet.
Hasseltia floribunda Kunth. 10,103; shrub or treelet.

Santalaceae
Dendrophthora turrialbae Kuijt. 10,071; parasitic shrub.
Phoradendron crassifolium (Pohl ex DC.) Eichler. 10,013, 10,073; parasitic shrub.

Sapindaceae
Allophylus psilospermus Radlk. 10,128, 9956, 9967; shrub or treelet.
Dilodendron costaricense (Radlk.) A.H. Gentry & Steyerm. 10,088, 10,345; emergent tree.
Dilodendron elegans (Radlk.) A. H. Gentry & Steyerm. 10,134; treelet.
Paullinia alata G. Don. 9969; woody vine.
Paullinia brenesii Croat. A. Weston 2473 (CR); woody vine.
Paullinia faginea (Triana & Planch.) Radlk. J. Utley 4949 (CR); woody vine.
Paullinia rugosa Benth. ex Radlk. 10,533, 10,156; woody vine.
Serjania caracasana (Jacq.) Willd. 9814; woody vine.
Serjania mexicana (L.) Willd. D. Norby 322 (CR); woody vine.
Serjania rhombea Radlk. 9978; woody vine.

Sapotaceae
Pouteria durlandii (Standl.) Baehni. 10,529, T. Pennington 11369 (CR); tree.
Pouteria torta (Mart.) Radlk. subsp. *tuberculata* (Sleumer) T.D.Penn. 10,400; emergent tree.

Schlegeliaceae
Schlegelia parviflora (Oerst.) Monach. 9936; woody vine.

Simaroubaceae
Simarouba amara Aubl. 10,003, 9933; tree.

Siparunaceae
Siparuna gesnerioides A.DC. 9818, 10,070; shrub or treelet.
Siparuna guianensis Aubl. 9918; shrub or treelet.
Siparuna thecaphora (Poepp. & Endl.) A.DC. 10,531; shrub or treelet.

Solanaceae
Acnistus arborescens Schltdl. 10,046; treelet.

Brugmansia suaveolens (Humb. & Bonpl. ex Willd.) Bercht. & J. Presl. 10,179; shrub.
Cestrum racemosum Ruiz & Pavon. 10,216; treelet or tree.
Juanulloa mexicana (Schltdl.) Miers. 10,185, 9893, 9951; epiphytic shrub.
Lycianthes beckneriana D'Arcy. 9831, 10,041; shrub.
Lycianthes multiflora Bitter. 9902; shrub.
Solanum circinatum Bohs. 10,118; shrub.
Solanum jamaicense Mill. 9908; shrub.
Solanum rugosum Dunal. 9876, 10372; shrub.
Solanum schlechtendalianum Walp. 9972, 10,012, 10,206; shrub.
Witheringia coccoloboides (Dammer) Hunz. 10,201; shrub.

Staphyleaceae

Turpinia occidentalis (Sw.) G. Don. 10,048, 10358, 10,068; tree.

Urticaceae

Cecropia obtusifolia Bertol. 10,250; treelet or tree.
Cecropia peltata L. 10,347, 10,561, 10086; treelet or tree.
Myriocarpa longipes Liebm. 9966; shrub or treelet.
Pourouma bicolor Mart. 9932, 10,098; emergent tree.

Verbenaceae

Citharexylum cooperi Standl. 10,186; shrub or treelet.
Lantana camara L. 10,037; shrub.
**Stachytarpheta mutabilis* (Jacq.) Vahl var. *violacea* Moldenke. 9825; shrub.

Vitaceae

Cissus brevipes C. V. Morton and Standl. 9937; woody vine.
Cissus cacuminus Standl. 10,234; woody vine.
Cissus erosa Rich. 9909; woody vine.
Cissus fuliginea Kunth. 9911; woody vine.

Vochysiaceae

Vochysia ferruginea Mart. 10,053; emergent tree
Vochysia guatemalensis Donn. Sm. 10,249; emergent tree.

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BOOK NOTICE

RONALD L. JONES & B. EUGENE WOFFORD. 2013. **Woody Plants of Kentucky & Tennessee: The Complete Winter Guide to Their Identification and Use.** (ISBN-13: 978-0-8131-4250-0, cloth; 978-0-8131-4309-5, epub; 978-0-8131-4310-1, web pdf). University Press of Kentucky, Editorial Offices, 663 South Limestone Street, Lexington, Kentucky 40508-4008, U.S.A. (**Orders:** www.kentuckypress.com, 1-800-537-5487). $45.00 US, 224 pp., 630 color photos, 2 maps, 57 figures, 7" × 10".

From the publisher: This comprehensive volume is the essential guide to woody plants in Kentucky, Tennessee, and surrounding states during the winter season. Featuring color images of more than four hundred species, this detailed botanical resource provides keys to the genera and species, as well as descriptions of the genera. The species accounts include useful information on Latin meanings, common names, habitats and distributions, and notes on toxicity, nativity, rarity, and wetland status. In addition, authors Ronald L. Jones and B. Eugene Wofford provide notes on practical uses for the plants, including food, medicine, fiber, and weapons.

Winter identification of woody plants can be a daunting exercise, but Jones and Wofford present clear and authoritative information that can help anyone spot these species in the wild. Whether taken into the field or enjoyed at home, *Woody Plants of Kentucky and Tennessee: The Complete Winter Guide to Their Identification and Use* is a comprehensive and accessible resource for professional and amateur botanists, students, commercial landscapers, homeowners, and outdoor enthusiasts.

Ronald L. Jones is foundation professor of biological sciences and curator of the herbarium at Eastern Kentucky University. He is the author of *Plant Life of Kentucky: An Illustrated Guide to the Vascular Flora*.

B. Eugene Wofford is research professor and director of the herbarium at the University of Tennessee. He is the author of *Guide to the Vascular Plants of the Blue Ridge* and coauthor of *Guide to the Trees, Shrubs, and Woody Vines of Tennessee*.

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CUSCATLANIA VULCANICOLA (NYCTAGINACEAE) NUEVO REGISTRO DEL GÉNERO Y ESPECIE PARA LA FLORA DE HONDURAS

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RESUMEN

Se registra por primera vez a *Cuscatlania vulcanicola* Standl. (Nyctaginaceae) para la flora de Honduras en las localidades de Locomapa (Departamento de Yoro) y Nuevo Celilac (Departamento de Santa Bárbara). Se describe la especie tal como ocurre en el país y se discuten datos de su hábitat y distribución geográfica.

Palabras clave: *Cuscatlania*, Nyctaginaceae, Locomapa, Yoro, Nuevo Celilac, flora de Honduras

ABSTRACT

Cuscatlania vulcanicola Standl. (Nyctaginaceae) is recorded for the first time for the flora of Honduras in the towns of Locomapa (Department of Yoro) and Nuevo Celilac (Department of Santa Bárbara). The species is described as it occurs in the country, and data of its habitat and geographical distribution are presented and discussed.

Key Words: *Cuscatlania*, Nyctaginaceae, Locomapa, Yoro, Nuevo Celilac, flora of Honduras

INTRODUCCIÓN

Durante el año 2010 se realizaron varias expediciones de colecta de plantas como parte de la consultoría de fortalecimiento de las capacidades botánicas del personal del Jardín Botánico Lancetilla. Una de estas expediciones tuvo lugar en la localidad de Locomapa, en el municipio y Departamento de Yoro. Mientras se hacían recorridos por algunos remanentes de bosque tropical caducifolio, se pudo observar un parche de vegetación muy bien conservado, con abundante cantidad de humus y ausencia de incendios, caracterizado por la presencia de especies que normalmente tardan muchos años en desarrollarse, como algunos cactus arborescentes del género *Cephalocereus* y *Opuntia*. Se realizaron algunas colectas de material fértil de diversas especies vegetales y entre éstas se colectaron algunos individuos de *Cuscatlania vulcanicola* Standl., de los cuales se prepararon varios duplicados de muestras de herbario.

El género *Cuscatlania* fue descrito por Standley (1923) de material procedente de la república de El Salvador. En ese entonces fue colectada en una quebrada rocosa del departamento de San Vicente en las faldas del volcán de San Vicente al oriente del país. Todo el material conocido, hasta su redescubrimiento y nuevo registro en 2014, pertenece a El Salvador (Linares et al. 2014).

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El redescubrimiento

Fue durante estos recorridos, realizados por parte de esa consultoría en julio de 2010, que en la localidad de Locomapa, Departamento de Yoro, se colectaron ejemplares de *Cuscatlania vulcanicola*. Asimismo, se pudo localizar un ejemplar de herbario de (*House et al. 5414*, depositado en el Herbario CURLA, Fig. 3) que, indudablemente representa a esta especie, con lo que se eleva a dos las localidades donde se presenta esta planta en el país. En Honduras, la familia Nyctaginaceae estaba representada sólo por tres géneros herbáceos, *Boerhavia, Salpianthus y Mirabilis* (Molina 1975; Nelson Sutherland 2008), y, con la adición de *Cuscatlania vulcanicola*, aumenta la diversidad de los géneros a cuatro. Dada la proximidad geográfica, se esperaría encontrar también a los géneros *Commicarpus*, presente en Guatemala (Standley & Steyermark 1946), *y Okenia*, presente en Nicaragua (Pool 2001). En este artículo se da a conocer el hallazgo de esta interesante planta, la cual representa un nuevo registro para la flora de Honduras, y se aumenta el área de distribución del género, conocido hasta ahora sólo en El Salvador (Fig. 1).

DESCRIPCIÓN DE LA ESPECIE

Cuscatlania vulcanicola Standl., J. Wash. Acad. Sci. 13(20):437. 1923. Tipo: El Salvador. Departamento de San Vicente: collected in a quebrada near the base of the Volcán de San Vicente, 500 m, mar 1922, *Standley 21678* (holotipo: US – Imagen!; isotipo: MO).

Hierba perenne, ascendente o decumbente, raíces actinomorfas, ligeramente engrosadas, ca. 2–3(–4) mm de grueso y cerca de 30 cm de largo; tallos ramificados, las ramitas 1–2mm, de grosor, glabras abajo y puberulentas o vilosas arriba; los tallos engrosados en los nudos, 2–3.5 mm de grosor, entrenudos más engrosados en la parte basal que en la distal, comúnmente de coloración rojiza; peciolos delgados, teretes, mayormente de 1–1.5 cm de largo, glabros o esparcidamente puberulentos; hojas opuestas, en pares muy desiguales, la pequeña menos de la mitad del tamaño de la mayor; la hoja mayor con margen entero, ovada a oblonga, ovada o lanceolado-oblonga, 5–12 cm de largo 3–4.5 cm de ancho, acuminada o largamente acuminada, muy desigual en la base, en un lado redondeada y en el otro aguda o atenuada, ligeramente carnosa, glabra o casi así, con numerosos y conspicuos rafidios en ambas superficies.

Flores sólo con el cáliz como único verticilo, pero semejando tener los dos verticilos debido a las brácteas sepaloides que lo rodean y a que el cáliz tiene una forma corolina o petaloide, es decir, semejando una corola típica. Perianto infundibuliforme, rojo, púrpura o magenta, casi 3 cm de largo, el tubo muy delgado, densamente viscoso, viloso con pelos muy cortos, ligeramente constreñido por arriba del ovario y caedizo, dando así la apariencia de un ovario ínfero, la limbo con forma de corola, 5-lobada; la garganta 3–4 mm de diámetro; estambres 3, los filamentos filiformes, ligeramente exertos, insertos en la pared del perianto , las anteras dídimas, blancas o amarillentas; ovario oblongo, estilo filiforme, exerto, el estigma capitado; antocarpo oblongo ovoide, constreñido en la base y en el ápice, casi 8 mm largo y 3 mm de diámetro, compuesto por la base endurecida del perianto, que encierra al utrículo, indehiscente y firmemente adherido a las paredes dando así la apariencia de un aquenio evidentemente 10-costillado, verruculoso con tricomas diminutos, el resto de la superficie muy esparcida y diminutamente hirtela, gris a casi negro. Inflorescencias cimosas, terminales o axilares, escasamente ramificadas o formando cimas compactas, con flores casmógamas y cleistógamas, las primeras terminales, la parte distal de la rama que precede a la inflorescencia con 6–8(–10) hojas reducidas, 1–2 cm de largo y 0.8–1.3 cm ancho, opuestas, subiguales, ovadas a cordadas, densamente víscido-vilosas, verde purpúreo en el haz y purpúreas en el envés, las inflorescencias individuales rodeadas por un involucro de 4–8 brácteas libres, lanceoladas u oblanceoladas a espatuladas, verde purpúreas, 10–15 mm largo y 2–3(–5) mm de ancho, pubescentes, viscosas (Fig. 1). Las flores cleistógamas axilares, generalmente dando la apariencia de pequeños apéndices claviformes, a menudo en grupos de 2–3 o a veces solitarios sostenidos por 4–8 brácteas involucrales, foliáceas, lanceoladas u oblanceoladas a oblongo-elípticas, 8–10 mm largo y 1–2(–3) mm de ancho, ápice agudo o acuminado, base atenuada, puberulenta.

Plántulas de germinación epigea, cotiledones aplanados, reniformes, suborbiculares u oblados, 16–20 mm de largo, 20–22 mm de ancho, verde-oscuros por el haz y purpúreos por el envés, primer par de eófilos opuestos, ovados, base redondeada, ápice agudo a acuminado, 13–15mm de largo por 9–11 mm de ancho.

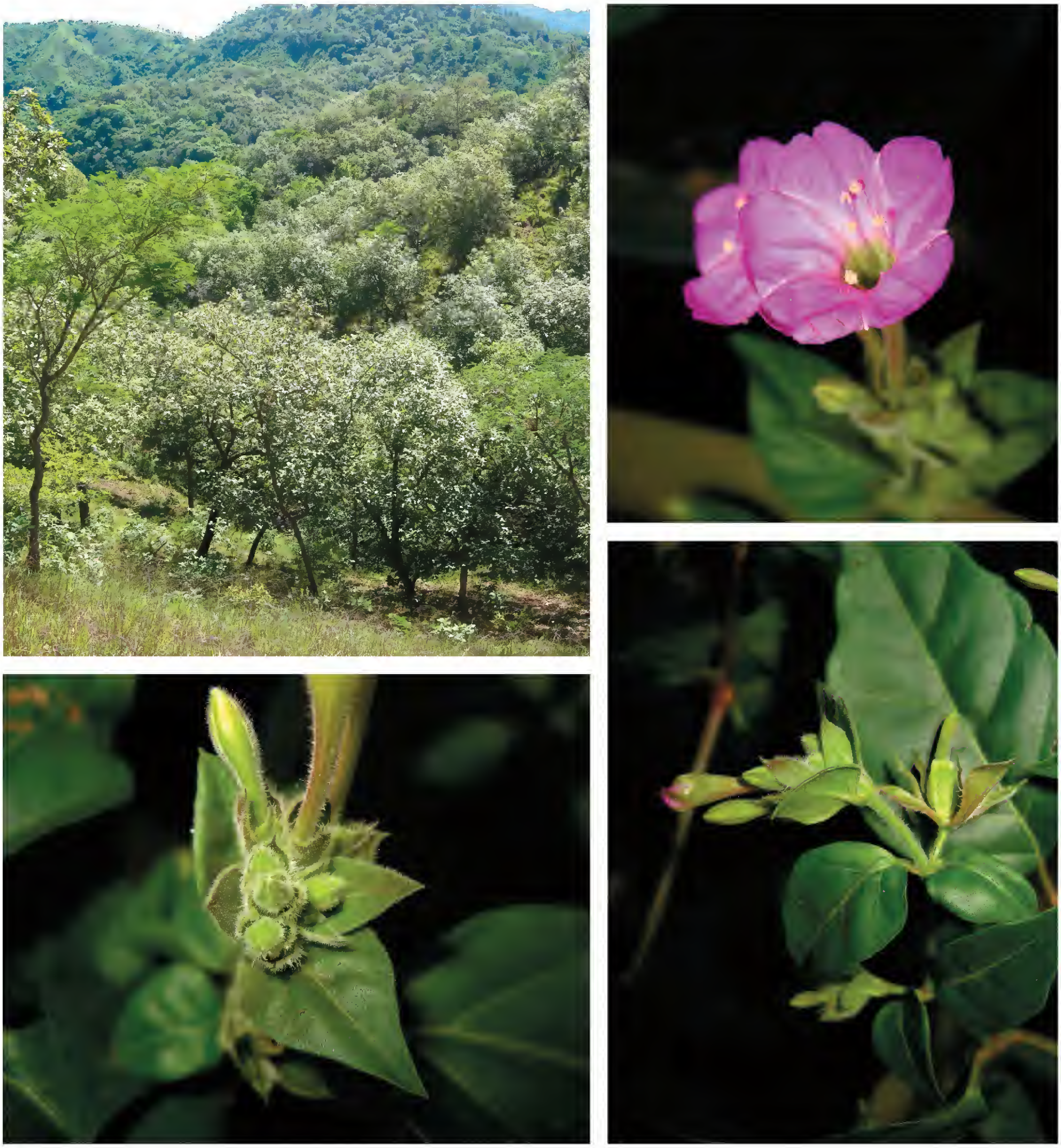


Fig. 1. A. Parche de vegetación en la localidad de Locomapa, Municipio y Departamento de Yoro, donde se encontró *Cuscatlania vulcanicola* Standl. **B.** Flores de *Cuscatlania vulcanicola* Standl. mostrando el perianto corolino y las anteras y estigma exerto. **C.** Inflorescencia lateral (presente todo el año), nótese la ausencia de hojas reducidas y la coloración verdosa de las brácteas y flores cleistógamas que no abren. **D.** Inflorescencia de "invierno" en la parte distal de la ramita. Nótese las hojas reducidas y de color purpúreo que preceden a la inflorescencia. La flor en el ápice de la rama muestra el perianto comenzando a tomar la forma y coloración corolina. Fotografías: Frank Sullyvan Cardoza Ruiz.

Hábitat.—Esta especie se conocía, como ya se mencionó, sólo de la colección tipo en el departamento de San Vicente, y fue redescubierta en 2008 en el Departamento de Santa Ana, ambos en El Salvador. En Honduras, *C. vulcanicola* se conoce sólo de un pequeño fragmento de selva baja caducifolia ubicada en la parte media de la cuenca del río Locomapa a ± 20 km al NO del municipio de Yoro y recientemente de otra localidad del bosque seco en el municipio de Nuevo Celilac, Departamento de Santa Bárbara. La localidad de Locomapa presenta especies de árboles típicos de este hábitat, como *Acacia pennatula* (Schltdl. & Cham.)

Benth., *Astronium graveolens* Jacq., *Bakeridesia molinae* D.M. Bates, *Cochlospermum vitifolium* (Willd.) Spreng., *Luehea candida* (Moc. & Sessé ex DC.) Mart., *Machaerium nicaraguense* Rudd, *Nopalea guatemalensis* Rose, *Randia aculeata* L., *Rondeletia deamii* (Donn. Sm.) Standl., *Spondias radlkoferi* Donn. Sm., *Tabebuia ochracea* (Cham.) Standl. y *Talisia oliviformis* (Kunth) Radlk. En el estrato herbáceo son comunes *Achyranthes aspera* L., *Boldoa purpurascens* Cav. ex Lag., *Petiveria alliacea* L. y *Rivinia humilis* L. La especie se desarrolla principalmente en suelos profundos, negros, ricos en materia orgánica y muy bien drenados, generalmente en lugares sombreados.

Fenología.—Los frutos originados de las flores casmógamas, aunque escasos, se pueden observar de finales de diciembre a principios de marzo; mientras que los originados de las flores cleistógamas son más abundantes y se pueden observar casi todo el año.

Material examinado.—**HONDURAS. Santa Bárbara:** Municipio de Nuevo Celilac, San Jerónimo del Pinal, bosque seco, 14°58'59"N; 87°16'53"O, 18 mar 2011, *Paul House et al. 5414* (CURLA). **Yoro:** Municipio de Yoro, Parte alta del valle de Locomapa, ca. 13 km al NO (en línea recta) de la ciudad de Yoro, cuenca del río Locomapa, a la orilla de la carretera Yoro - Locomapa, 15°14'50"N y 87°14'08"N, 675 msnm, 10 jul 2010, *J.L. Linares et al. 14402* (JBL, MEXU) (Fig. 2 y 3).

Etimología.—El nombre del género, *Cuscatlania*, acuñado por Paul Carpenter Standley (1884-1963), viene de Cuscatlán, nombre de origen náhuatl con que se conoce a El Salvador (Amaroli 1986), en alusión a que fue encontrado originalmente en esa república; mientras que el nombre de la especie, *vulcanicola,* es una palabra de

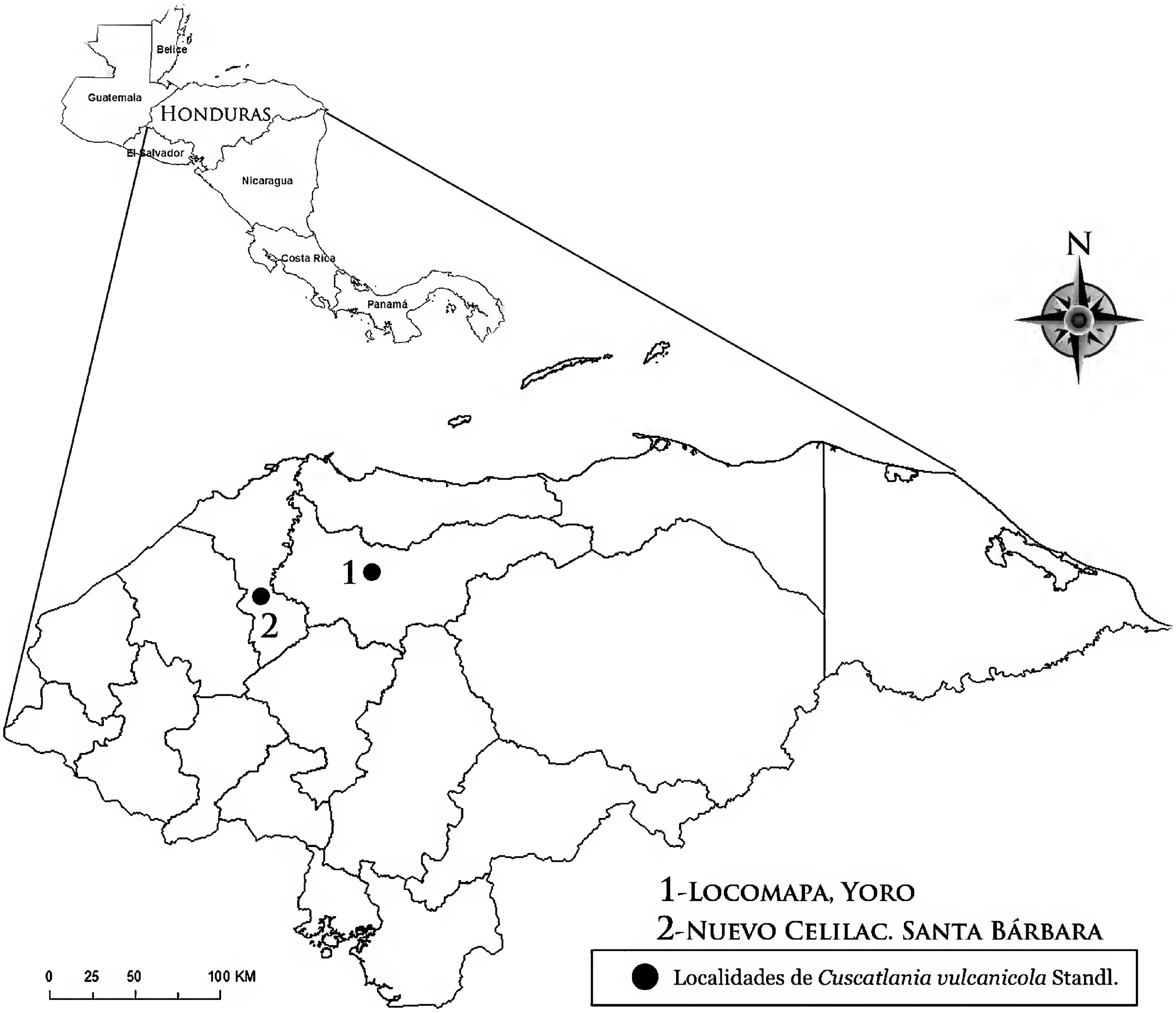
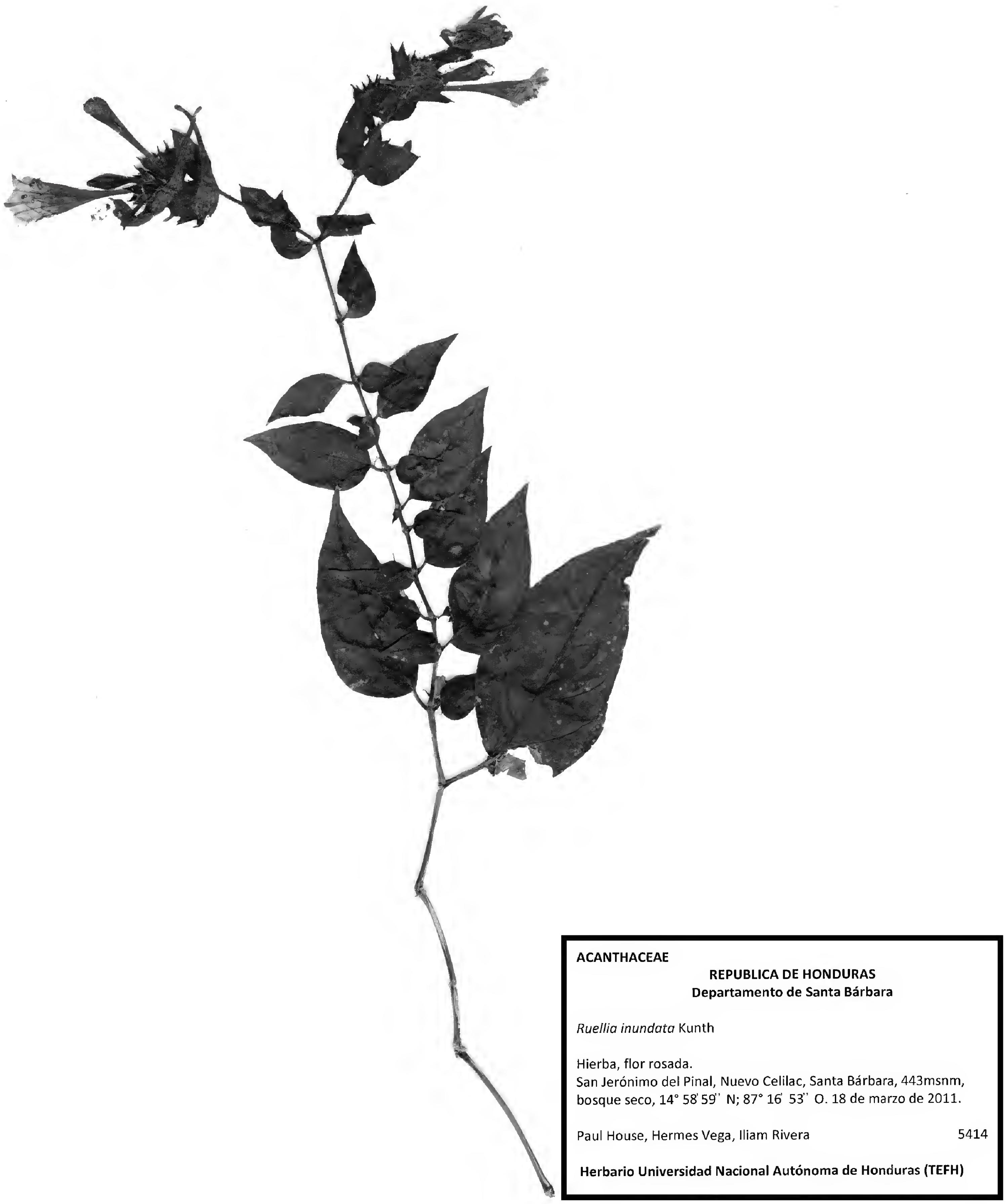


Fig. 2. Distribución geográfica y localidades en Honduras de *Cuscatlania vulcanicola* Standl..



ACANTHACEAE

REPUBLICA DE HONDURAS
Departamento de Santa Bárbara

Ruellia inundata Kunth

Hierba, flor rosada.
San Jerónimo del Pinal, Nuevo Celilac, Santa Bárbara, 443msnm, bosque seco, 14° 58' 59'' N; 87° 16' 53'' O. 18 de marzo de 2011.

Paul House, Hermes Vega, Iliam Rivera 5414

Herbario Universidad Nacional Autónoma de Honduras (TEFH)

Fig. 3. Ejemplar de herbario de *Cuscatlania vulcanicola* Standl, determinada por el autor.

origen latino compuesta de *vulcanus volcán*, e *incola* habitante, en alusión a que fue encontrada originalmente en las faldas del volcán San Vicente o Chinchontepec de El Salvador.

Comentarios.—La apariencia general es similar a la de algunas especies del género *Allionia* (de Norte y Sudamérica) o al de *Mirabilis* (de América tropical y subtropical) con los cuales indudablemente está relacionado (Standley 1923). *Cuscatlania vulcanicola* se distingue por la inserción de los estambres en la pared del tubo del perianto (y no en la base), siendo ésta una característica única en toda la familia (Standley 1923). Esta especie es muy fácilmente distinguible por la siguiente combinación de características:

A. Hojas opuestas, en pares anisofilos, de los cuales la hoja mayor es más de dos veces más grande que la menor, base asimétrica.

B. Brácteas involucrales libres 4–8, sosteniendo 1–2 flores de perianto infundibuliforme, rojo, púrpura o magenta, con los estambres insertos en la pared del perianto.

CLAVE PARA LOS GÉNEROS DE LAS NYCTAGINACEAE HERBÁCEAS PRESENTES (O ESPERADAS) EN HONDURAS

1. Hojas alternas ______ **Boldoa**
1. Hojas opuestas, sub opuestas, verticiladas o fasciculadas.
   2. Antocarpo hipogeo; flores con (9–)14–19 estambres ______ **Okenia** (presente en Nicaragua, esperado en Honduras)
   2. Antocarpo epígeo; flores con 1–5 estambres.
      3. Brácteas fusionadas en la base en un involucro parecido a un cáliz lobado; perianto ca 8–80 mm de largo ______ **Mirabilis**
      3. Brácteas libres, a veces muy próximas entre sí, pero nunca fusionadas, perianto 1.5–30 mm de largo.
         4. Perianto ca 30 mm de largo o más, brácteas involucrales ______ **Cuscatlania**
         4. Perianto 1.5–3 mm de largo, brácteas no involucrales.
            5. Plantas perennes, hierbas leñosas o arbustos, reclinadas o trepando sobre arbustos, muy ramificadas y leñosas en la parte basal; inflorescencias umbeladas, largamente pedunculadas, perianto blanco o blanco verdoso ______ **Commicarpus** (presente en Guatemala, esperado en Honduras)
            5. Plantas herbáceas anuales o perennes, postradas o erectas, nunca trepadoras, poco ramificadas en la base, inflorescencias cortamente umbeladas, cáliz rojo púrpura, blanquecino o rosado ______ **Boerhavia**

CONCLUSIONES

En referencia al estado de conservación de esta especie, el alto grado de deterioro y fragmentación de su hábitat la hacen poco frecuente, y se considera extinta en otras zonas similares del país. De acuerdo con los criterios de la *Lista Roja de Especies Amenazadas* (UICN 2012), y según las observaciones de los autores, estas plantas son raras y poco comunes, siendo la categoría para esta especie la de Vulnerable, VU A1(d).

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STRUCTURAL ANALYSIS OF SHRUBLANDS ADJACENT TO THE MONTERREY METROPOLITAN AREA, MEXICO

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ABSTRACT

Four communities of shrublands adjacent to the Monterrey Metropolitan Area of the state of Nuevo Leon, northeastern Mexico were studied. The values of abundance, coverage, relative importance value (*RIV*), and dominance-diversity of all arboreal, shrubs, and succulent species were recorded. An inventory of species was carried out with respect to height and diameter of individual specimens with basal stem diameter of 1 cm or greater. A total of 84 species, 68 genera, and 30 families were recorded. The most representative family in three plant communities was Fabaceae. The species with the highest *RIV* were *Agave lecheguilla* (Lechuguilla agave, rosetophyllous desert shrubland), *Cordia boissieri* (Texas Wild Olive, tamaulipan thornscrub and semithorn shrubland), and *Acacia rigidula* (Blackbush Acacia, piedmont scrub). Plant communities were composed primarily of two strata: low and medium shrubs. Communities with higher aerial coverage were tamaulipan thornscrub and piedmont scrub. According to the species dominance-diversity curve, it was determined that the communities were at mature successional stage.

Key Words: Fabaceae, tamaulipan thornscrub, piedmont scrub

RESUMEN

Se estudiaron cuatro comunidades de matorrales adyacentes al Área Metropolitana de Monterrey del estado de Nuevo León en el noreste de México. Se registraron los valores de abundancia, cobertura, valor de importancia relativa (*VIR*) y la diversidad-dominancia de las especies arbóreas, arbustivas y suculentas presentes. Se llevó cabo un inventario de las especies considerando mediciones de altura y diámetro de los individuos mayores o iguales a 1 centímetro de diámetro basal. Se registraron un total de 84 especies, 68 géneros y 30 familias. La familia más representativa en tres de las comunidades fue Fabaceae. Las especies con los valores de VIR más altos fueron *Agave lecheguilla* (agave lechuguilla, matorral desértico rosétofilo), *Cordia boissieri* (matorral espinoso tamaulipeco y matorral subinerme) y *Acacia rigidula* (matorral submontano). Las comunidades vegetales están conformadas principalmente por dos estratos: arbustos bajos y medianos. Las comunidades con mayor cobertura aérea fueron el matorral espinoso tamaulipeco y matorral submontano. De acuerdo con la curva de dominancia-diversidad de las especies, se determinó que las comunidades se encuentran en estadío sucesional maduro.

Palabras clave: Fabaceae, matorral espinoso tamaulipeco, matorral submontano

INTRODUCTION

Despite the vast territory occupied by desert areas, from year to year they are affected by changes in land use which are the result of human activities such as rail and road infrastructures and urban development, agriculture, livestock, mining, and tourism (Ewing & Best 2004; Arriaga 2009; Alanis et al. 2013). These changes in land use disturb the physical and biological environment by soil erosion, habitat modification, biological interactions of wild populations, animal behavior, ecosystem processes, and acceleration of the introduction of invasive species and the increase in the fragmentation of rural and urban areas (Arriaga 2009; Alix-Garcia et al. 2010; Krauss et al. 2010; Vranckx et al. 2012).

With respect to globally registered wilderness, arid and semi-arid areas of Mexico are at risk of decreasing their coverage in the short-term future which will affect the most productive areas (Bonilla et al. 2013) with the disadvantage that their biodiversity and ecosystem processes are poorly studied (Alanis et al. 2013) or unknown for some regions (Arriaga 2009).

The piedmont scrub, microphyllous desert scrub, and rosetophyllous desert shrubland are among the vegetation types that have been recorded with a high species richness (Arriaga 2009; Canizales et al. 2009; Encina et al. 2013; Alanis et al. in press). Despite their lesser abundance than in the humid and tropical regions, plants in the arid and semi-arid areas of northern Mexico have evolved a rich and distinctive flora presenting highly specialized growth forms that are generally unique (Rzedowski 1978).

According to the INEGI classification (2005), 14 types of scrub ecosystem are found in Mexico, most of them widespread in the north of the country. In regard to the state of Nuevo Leon, northeastern Mexico, the following five scrub communities are registered as: semithorn shrubland (SS), rosetophyllous desert shrubland (RDS), piedmont scrub (PS), tamaulipan thornscrub (TT), and microphyllous desert scrub (MDS).

In this work, we studied four of the five most common types of shrublands found in the state of Nuevo Leon (SS, RDS, PS, and TT) to determine their structure including their plant density (N/ha), plant coverage (m^2/ha), frequency, relative importance value (RIV)and dominance-diversity graph. The increase in the rate of population growth, that of the peripheral municipalities of the Monterrey Metropolitan Area, has resulted in a big impact on nature (Alanis 2005). Knowledge of the structure of these plant communities will contribute to promoting a strategic planning with respect to conservation and sustainable management of these areas that are currently heavily affected by anthropogenic activities.

MATERIALS AND METHODS

Study area.—The present study was carried out in an area of shrublands adjacent to the Monterrey Metropolitan Area of the state of Nuevo Leon, northeastern Mexico (25°09'–24°33'N, 99°07'W) which covers twelve municipalities of the state of Nuevo Leon, has an area of 6,680 m^2 (SEDESOL et al. 2007), located between the physiographic zones Gulf Coastal Plain and the Sierra Madre Oriental, with an altitude of 534 ma.s.l. The characteristic climate is dry steppe, warm and extreme, with an annual average temperature of 22.1°C, with irregular rainfall in late summer and a precipitation of 634 mm (Cervantes & Merla 1995). The study areas were within the Monterrey Metropolitan Area in the municipalities of Monterrey (SS and PS), Santa Catarina (RDS) and Salinas Victoria (TT) (Fig. 1).

Woody species with high abundance and cover are: *Acacia rigidula, Acacia farnesiana, Havardia pallens, Cordia boissieri, Karwinskia humboldtiana,* and *Prosopis glandulosa* (Espinoza & Navar 2005; Alanis et al. 2008; Jimenez et al. 2009). Table 1 presents some physical and climatic variables as a description of the studied areas.

Sampling methods.—In the years 2010 and 2011, 25 sampling plots with sizes of 100 m^2 (10 m × 10) were established in each shrubland, resulting in a total of 100 plots for characterizing the vegetation. The distribution of the sampling plots was systematic with a distance of 50 m between them. According to the species-area curve, community SS presented a minimum of 25 sites, while the other communities displayed a fewer sampling plots. For the statistical analysis, we established the same number of sampling plots for each community. A square shape was used for each plot because this shape made it easier to layout and measure structural attributes of vegetation in the studied sites (Canizales et al. 2009). In each sampling plot, an inventory of all of the woody species was performed, including measurements such as determination of the plant coverage (m^2) and stem diameter (cm) at 10 cm ($d0.10 \geq 1$ cm). Diameter measurements were performed 0.10 m above the soil surface, which represents a standard measurement used for woody species in TT (Alanis et al. 2008; Jimenez et al. 2009). The canopy cover was also measured based on the four cardinal points of the north-south and east-west directions.

We analyzed relative abundance, dominance, relative importance value (*RIV*), and mean height of woody individuals. The absolute abundance is $Ai = Ni/S$, where Ni is the number of individuals of species i and S is the sample surface (in hectares). The relative abundance of species was calculated using the equation $Ari =$

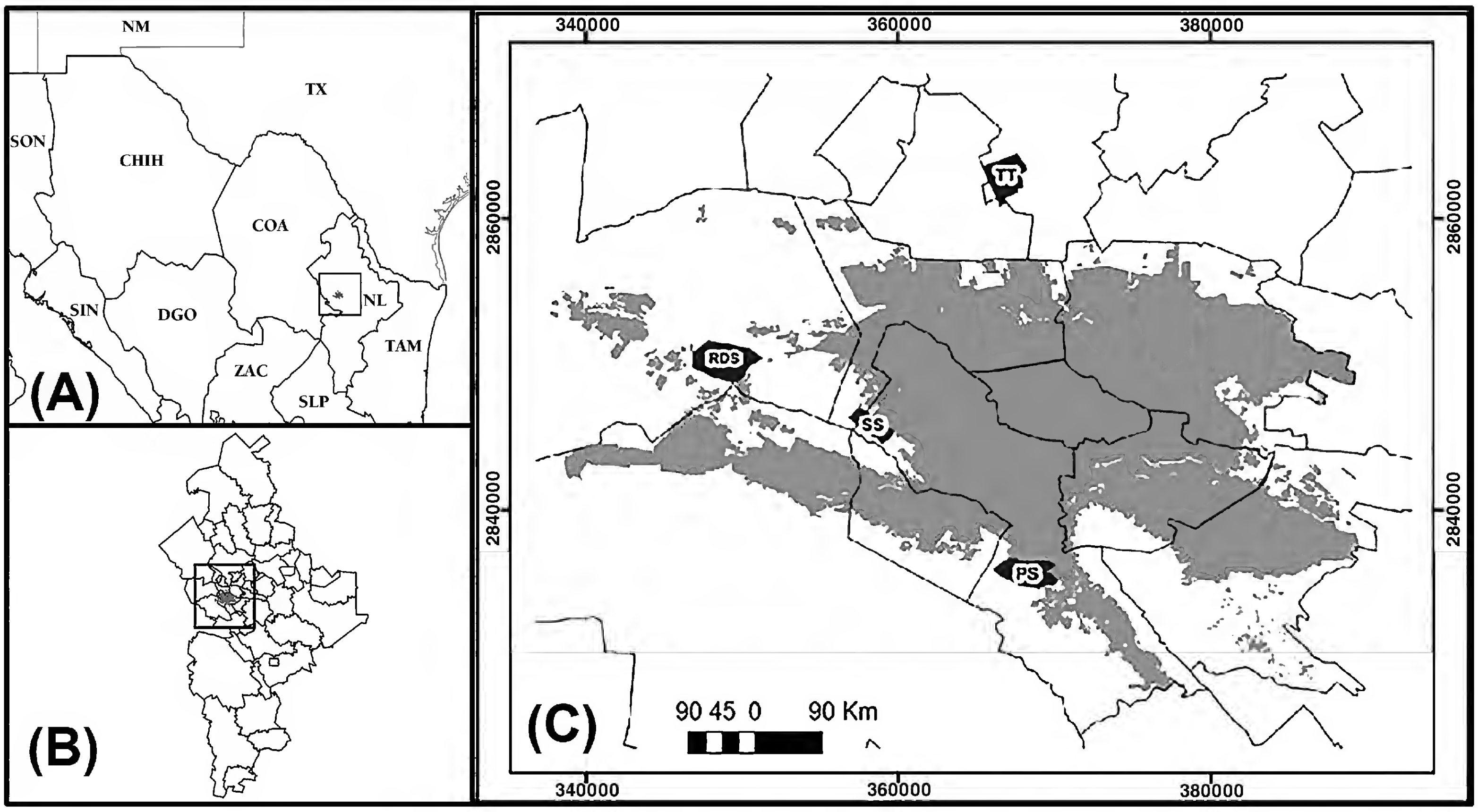

Fig. 1. Location of the study areas. A) North of Mexico and south of USA, B) Nuevo Leon state, northeastern Mexico, and C) municipalities of the Monterrey Metropolitan Area, in addition to the study areas: TT, tamaulipan thornscrub, SS, semithorn shrubland, PS, piedmont scrub, RDS, rosetophyllous desert shrubland.

Table 1. Description of assessed areas.

Vegetation	Tamaulipan thornscrub	Semithorn shrubland	Piedmont scrub	Rosetophyllous desert shrubland
Abbreviation	TT	SS	PS	RDS
Coordinates (MTU)	368638 E 2866744 N	358755 E 2845296 N	369795 E 2832599 N	342616 E 2842694 N
Altitude (meters above sea level)	480	850	660	640
Mean annual temperature (oC)	20 to 22	20 to 22	18 to 20	18 to 20
Mean annual precipitation (mm)	400 to 600	300 to 600	400 to 600	125 to 300
Soil type	Luvic Xerosols	Lithosols Rendzinas	Lithosols Vertisols	Regosols Xerosols

t($Ai/\Sigma Ai$)/100, where ΣAi is the total abundance of species i (Jimenez et al. 2009). To estimate dominance, the basal area for each individual was calculated. The absolute dominance of species is $Di = Abi/S$, where Abi is the cover area (in square meters) of species i and S is the sample surface (in hectares). The relative dominance of species was calculated using the equation $Dri = (Di/\Sigma Di)/100$, where Di is as aforementioned and ΣDi is the total dominance of species. The relative frequency is $Fri = (Fi/\Sigma Fi)/100$, where Fi is the number of sites that present the species i and $\Sigma\Sigma Fi$ is the total frequency of all species (Mostacedo & Fredericksen 2000). The relative importance value (*RIV*; Müeller-Dombois & Ellenberg 1974).) was calculated according to the following formula:

$$\mathbf{RIV} = \frac{\textbf{Relative abundance + relative dominance + relative frequency}}{\mathbf{3}}$$

The structure of the community was described in terms of the proportional abundance of species using a diversity-abundance graph which shows the graphical relationship between the importance value of species (on a logarithmic scale) as a function of an array sequence of species ranging in importance from most to least (Martella et al. 2012).

RESULTS

According to the four plant communities studied, a total of 84 plant species were recorded including 68 genera and 30 families (Table 2). Six forms of life were recorded: trees, shrubs, succulents, grasses, rosettes, and vines.

A number of 18 families were found in the Tamaulipan thornscrub. The most representative families were Fabaceae and Cactaceae with 8 and 4 species, respectively. A total of 29 species was recorded including *Cordia boissieri* (14.96%), *Leucophyllum frutescens* (13.29%), and *Gymnosperma glutinosum* (12.22%), which were the most abundant, but it is noteworthy that none of these species belongs to the above-mentioned representative families. The species with the highest frequency was *Cordia boissieri* (10.13%). The dominant life form was low scrub (≤ 1.5 m) with 57% while the average recorded height was 1.86 m.

Eighteen families were recorded within the semithorn shrubland, and the most representative was Fabaceae with 10 species. There was a total of 34 other species in this shrubland, and the most abundant were *Acacia rigidula* (12.03%), *Leucophyllum frutescens* (11.05%), and *Bernadia myricifolia* (9.75%). The most prevalent species in this community was *Cordia boissieri* (7.85%). The low and medium shrubs were the main form of life, which accounted for 96% of individuals present in this community with an average height of 1.85 m.

Nineteen families were recorded in the piedmont scrub with over 34 species. The most representative was Fabaceae with 9 species, and *Acacia rigidula* was the most abundant species with 45.50%. With respect to the highest relative frequency, *Acacia rigidula* and *Zanthozylum fagara* both had 11.27%. The highest average height recorded for this community was 2.54 m. Medium shrubs were the dominant life form with 69% of individuals.

Sixteen families and 48 species were recorded in the rosetophyllous desert shrubland. The most representative was Cactaceae with 17 species, followed by Fabaceae with 6 species and Asteraceae and Asparagaceae with 5 species, respectively. The most abundant and frequent species with 26.82% and 8.26%, respectively, was *Agave lecheguilla*. In this community, the predominant categories were ground vegetation (41%) and low shrubs (54%) with species types such as rosette and succulents, cacti being the most prevalent of the latter.

Frequencies evaluated for the *RIV* distribution of the ecosystem are shown in Figure 2. There is a decrease in the number of species with respect to increasing percentage values of *RIV*, and classes of <2% of the *RIV* showed the higher number of species, indicating a high number of species with little ecological weight and conversely a small number of species with high ecological weight.

Tree covers for TT (13,718.68 m^2/ha) and PS (17,267.78 m^2/ha) communities were greater while covers for SS (8,138.43 m^2/ha) and RDS (8,710.46 m^2/ha) were similar, but with lower values. This corresponds to the predominant way of life in the communities as the shrub forms (low and medium) representing greater coverage in communities such as TT and PS, while the forms of life which are predominantly semithorn shrubland (SS) and rosetophyllous desert shrubland (RDS) represent less coverage (Fig. 3).

The shape of the dominance-diversity of species curve (Fig. 4) behaves as a typical log-normal curve. This distribution is based on the number of individuals per species (on a logarithmic scale) which follows a normal distribution whereby individuals of intermediate abundance are common and there are few species with very high or low values of abundance (Magurran 1988).

DISCUSSION

The most representative family for the Tamaulipan thornscrub community was Fabaceae with eight species, which agrees with previous studies developed Mora et al. (2013) and Molina et al. (2013) who also recorded eight species of Fabaceae, the former for a community with a history of agriculture/livestock use. Other researchers reporting the same information include Jimenez et al. (2012), Gonzalez et al. (2010), Alanis et al. (2013), and Foroughbakch et al. (2013). *Cordia boissieri* was frequently the most abundant species, in contrast to what was reported by other authors who recorded *Acacia rigidula* as the most abundant species of TT (Gonzalez et al. 2010; Navar & Espinoza 2005). Meanwhile Jimenez et al. (2012), Alanis et al. (2013), and Mora

Table 2. Abundance, frequency, dominance and *RIV* in the communities assessed.

Species	No.	Abundance (N/ha) Absolute	Relative	Frequency Absolute	Dominance (m^2-ha) Relative	Absolute	Relative	RIV (%)
TAMAULIPAN THORNSCRUB								
Asparagaceae								
Yucca filifera Chabaud	4	16	0.39	3	1.32	165.88	1.21	0.97
Asteraceae								
Gymnosperma glutinosum (Spreng.) Less.	125	500	12.22	15	6.61	253.01	1.84	6.89
Berberidaceae								
Berberis trifoliolata Moric.	57	228	5.57	9	3.96	42.41	0.31	3.28
Boraginaceae								
Cordia boissieri A. DC.	153	612	14.96	23	10.13	4481.90	32.67	19.25
Cactaceae								
Coryphantha neglecta L. Bremer	2	8	0.20	2	0.88	1.41	0.01	0.36
Cylindropuntia leptocaulis (DC.) F.M. Knuth.	21	84	2.05	11	4.85	31.91	0.23	2.38
Echinocereus stramineus (Engelm.) F. Seitz	2	8	0.20	2	0.88	64.30	0.47	0.52
Opuntia engelmannii Salm-Dyck ex Engelm.	18	72	1.76	10	4.41	193.66	1.41	2.53
Euphorbiaceae								
Croton torreyanus Müll.Arg.	6	24	0.59	2	0.88	24.86	0.18	0.55
Fabaceae								
Acacia farnesiana (L.) Willd.	1	4	0.10	1	0.44	33.16	0.24	0.26
Acacia greggii A. Gray	1	4	0.10	1	0.44	6.60	0.05	0.20
Acacia rigidula Benth.	2	8	0.20	1	0.44	28.01	0.20	0.28
Cercidium macrum I.M. Johnst.	15	60	1.47	2	0.88	126.76	0.92	1.09
Eysenhardtia polystachya (Ortega) Sarg.	6	24	0.59	4	1.76	43.51	0.32	0.89
Havardia pallens (Benth.) Britton & Rose	35	140	3.42	6	2.64	1653.61	12.05	6.04
Prosopis leavigata (Humb. & Bonlp. ex Willd.) M.C. Johnst.	3	12	0.29	2	0.88	356.28	2.60	1.26
Koeberliniaceae								
Koeberlinia spinosa Zucc.	2	8	0.20	2	0.88	26.45	0.19	0.42
Oleaceae								
Forestiera angustifolia Torr.	8	32	0.78	6	2.64	115.79	0.84	1.42
Rhamnaceae								
Karwinskia humboldtiana (Schult.) Zucc.	24	96	2.35	11	4.85	94.85	0.69	2.63
Rutaceae								
Zanthoxylum fagara (L.) Sarg.	93	372	9.09	20	8.81	1372.76	10.01	9.30
Salicaceae								
Neopringlea integrifolia (Hemsl.) S. Watson	2	8	0.20	1	0.44	3.18	0.02	0.22
Scrophulariaceae								
Leucophyllum frutescens (Berland.) I.M. Johnst.	136	544	13.29	21	9.25	903.45	6.59	9.71
Simaroubaceae								
Castela erecta subsp. *texana* (Torr. & A.Gray) Cronquist	26	104	2.54	8	3.52	78.40	0.57	2.21
Solanaceae								
Capsicum annuum L.	1	4	0.10	1	0.44	3.46	0.03	0.19
Ulmaceae								
Celtis leavigata Willd.	53	212	5.18	7	3.08	1597.97	11.65	6.64
Celtis pallida Torr.	61	244	5.96	16	7.05	1159.82	8.45	7.16
Verbenaceae								
Aloysia sp.	18	72	1.76	4	1.76	91.91	0.67	1.40
Lantana camara L.	117	468	11.44	20	8.81	650.91	4.74	8.33
Zygophyllaceae								
Guaiacum angustifolium Engelm.	31	124	3.03	16	7.05	112.48	0.82	3.63
Total	**1023**	**4092**	**100.00**	**227**	**100.00**	**13,718.68**	**100.00**	**100.00**

Table 2. (continued)

Species	No.	Abundance (N/ha) Absolute	Relative	Frequency Absolute	Dominance (m^2-ha) Relative	Absolute	Relative	RIV (%)
				SEMITHORN SHRUBLAND				
Asparagaceae								
Agave lecheguilla Torr.	6	24	0.65	4	1.37	15.99	0.20	0.74
Yucca filifera Chabaud	27	108	2.93	16	5.46	952.10	11.70	6.69
Asteraceae								
Gymnosperma glutinosum (Spreng.) Less.	49	196	5.31	15	5.12	166.77	2.05	4.16
Boraginaceae								
Cordia boissieri A. DC.	67	268	7.26	23	7.85	1302.85	16.01	10.37
Ehretia anacua (Teran & Berland.) I.M. Johnston	5	20	0.54	2	0.68	16.43	0.20	0.48
Cactaceae								
Opuntia engelmannii Salm-Dyck ex Engelm.	13	52	1.41	8	2.73	49.92	0.61	1.58
Ebenaceae								
Diospyros texana Scheele	25	100	2.71	12	4.10	731.68	8.99	5.26
Euphorbiaceae								
Bernardia myricifolia (Scheele) S. Watson	90	360	9.75	16	5.46	399.06	4.90	6.70
Croton torreyanus Müll.Arg.	72	288	7.80	21	7.17	492.47	6.05	7.01
Fabaceace								
Acacia berlandieri Benth.	30	120	3.25	10	3.41	121.55	1.49	2.72
Acacia greggii A. Gray	9	36	0.98	3	1.02	56.04	0.69	0.90
Acacia rigidula Benth.	111	444	12.03	22	7.51	464.03	5.70	8.41
Caesalpinia mexicana A. Gray	5	20	0.54	3	1.02	16.21	0.20	0.59
Ebenopsis ebano (Berland.) Baneby & J.W. Grimes	3	12	0.33	1	0.34	2.10	0.03	0.23
Eysenhardtia polystachya (Ortega) Sarg.	60	240	6.50	14	4.78	321.90	3.96	5.08
Havardia pallens (Benth.) Britton & Rose	5	20	0.54	3	1.02	155.98	1.92	1.16
Prosopis glandulosa Torr.	1	4	0.11	1	0.34	143.07	1.76	0.74
Sophora secundiflora (Ortega) DC.	8	32	0.87	4	1.37	49.01	0.60	0.94
Mimosa malacophylla A. Gray	6	24	0.65	2	0.68	19.15	0.24	0.52
Fouquieriaceae								
Fouquieria splendens Engelm.	11	44	1.19	3	1.02	112.51	1.38	1.20
Oleaceae								
Forestiera angustifolia Torr.	17	68	1.84	11	3.75	66.34	0.82	2.14
Bumelia lanuginosa (Michx.) Pers.	6	24	0.65	2	0.68	27.09	0.33	0.56
Rhamnaceae								
Condalia hookeri M.C. Johnst.	26	104	2.82	5	1.71	878.65	10.80	5.11
Karwinskia humboldtiana (Schult.) Zucc.	17	68	1.84	10	3.41	35.27	0.43	1.90
Rubiaceae								
Randia laetevirens Standl.	3	12	0.33	3	1.02	7.55	0.09	0.48
Rutaceae								
Zanthoxylum fagara (L.) Sarg.	53	212	5.74	19	6.48	319.59	3.93	5.38
Salicaceae								
Neopringlea integrifolia (Hemsl.) S. Watson	11	44	1.19	3	1.02	14.08	0.17	0.80
Scrophulariaceae								
Leucophyllum frutescens (Berland.) I.M. Johnst.	102	408	11.05	21	7.17	891.88	10.96	9.73
Ulmaceae								
Celtis leavigata Willd.	11	44	1.19	5	1.71	5.12	0.06	0.99
Celtis pallida Torr.	10	40	1.08	5	1.71	59.74	0.73	1.17
Verbenaceae								
Lantana camara L.	44	176	4.77	15	5.12	144.99	1.78	3.89
Zygophyllaceae								
Guaiacum angustifolium Engelm.	10	40	1.08	4	1.37	33.94	0.42	0.96
Without identification								
sp1	7	28	0.76	4	1.37	57.14	0.70	0.94
sp2	3	12	0.33	3	1.02	8.25	0.10	0.48
Total	**923**	**3692**	**100.00**	**293**	**100.00**	**8138.43**	**100.00**	**100.00**

Table 2. (continued)

Species	No.	Abundance (N/ha) Absolute	Relative	Frequency Absolute	Dominance (m^2-ha) Relative	Absolute	Relative	RIV (%)
		PIEDMONT SCRUB						
Anacardiaceae								
Rhus microphylla Engelm.	24	96	2.12	2	0.98	65.36	0.38	1.16
Boraginaceae								
Cordia boissieri A. DC.	54	216	4.76	13	6.37	1066.74	6.18	5.77
Ehretia anacua (Teran & Berland.) I.M. Johnston	24	96	2.12	9	4.41	1005.51	5.82	4.12
Cactaceae								
Opuntia engelmannii Salm-Dyck ex Engelm.	14	56	1.23	8	3.92	44.17	0.26	1.80
Ebenaceae								
Diospyros texana Scheele	74	296	6.53	19	9.31	1653.56	9.58	8.47
Diospyros virginiana L.	2	8	0.18	2	0.98	25.12	0.15	0.43
Euphorbiaceae								
Bernardia myricifolia (Scheele) S. Watson	13	52	1.15	2	0.98	68.55	0.40	0.84
Croton torreyanus Müll.Arg.	8	32	0.71	3	1.47	17.66	0.10	0.76
Fabaceae								
Acacia berlandieri Benth.	6	24	0.53	4	1.96	121.27	0.70	1.06
Acacia farnesiana (L.) Willd.	24	96	2.12	4	1.96	552.04	3.20	2.42
Acacia rigidula Benth.	516	2064	45.50	23	11.27	5420.23	31.39	29.39
Caesalpinia mexicana A. Gray	51	204	4.50	13	6.37	227.93	1.32	4.06
Eysenhardtia texana Scheele	5	20	0.44	4	1.96	44.10	0.26	0.89
Leucaena sp.	4	16	0.35	2	0.98	0.85	0.00	0.45
Mimosa malacophylla A. Gray	6	24	0.53	4	1.96	27.62	0.16	0.88
Havardia pallens (Benth.) Britton & Rose	16	64	1.41	2	0.98	140.05	0.81	1.07
Sophora secundiflora (Ortega) DC.	3	12	0.26	1	0.49	3.31	0.02	0.26
Fagaceae								
Quercus polymorpha Schltdl. & Cham.	30	120	2.65	6	2.94	140.27	0.81	2.13
Lythraceae								
Heimia salicifolia (Kunth) Link	2	8	0.18	2	0.98	4.54	0.03	0.39
Lauraceae								
Litsea novoleontis Bartlett	20	80	1.76	4	1.96	1901.19	11.01	4.91
Oleaceae								
Forestiera angustifolia Torr.	32	128	2.82	14	6.86	394.67	2.29	3.99
Fraxinus americana L.	4	16	0.35	2	0.98	155.75	0.90	0.75
Rhamnaceae								
Condalia hookeri M.C. Johnst.	4	16	0.35	2	0.98	11.66	0.07	0.47
Karwinskia humboldtiana (Schult.) Zucc.	8	32	0.71	3	1.47	25.86	0.15	0.78
Rubiaceae								
Randia laetevirens Standl.	12	48	1.06	4	1.96	107.17	0.62	1.21
Rutaceae								
Zanthoxylum fagara (L.) Sarg.	127	508	11.20	23	11.27	2429.38	14.07	12.18
Sapindaceae								
Sapindus saponaria L.	2	8	0.18	2	0.98	33.22	0.19	0.45
Sapotaceae								
Bumelia lanuginosa (Michx.) Pers.	12	48	1.06	5	2.45	103.91	0.60	1.37
Scrophulariaceae								
Leucophyllum frutescens (Berland.) I.M. Johnst.	9	36	0.79	3	1.47	62.72	0.36	0.88
Solanaceae								
Solanum erianthum D. Don	2	8	0.18	2	0.98	2.65	0.02	0.39
Ulmaceae								
Celtis leavigata Willd.	10	40	0.88	6	2.94	398.51	2.31	2.04
Celtis pallida Torr.	6	24	0.53	6	2.94	63.19	0.37	1.28
Ulmus crassifolia Nutt.	8	32	0.71	3	1.47	947.76	5.49	2.55
Verbenaceae								
Lantana camara L.	2	8	0.18	2	0.98	1.27	0.01	0.39
Total 1134	**4536**	**100.00**	**204**	**100.00**	**17,267.78**	**100.00**	**100.00**	

Table 2. (continued)

Species	No.	Abundance (N/ha) Absolute	Relative	Frequency Absolute	Dominance (m^2-ha) Relative	Absolute	Relative	RIV (%)
ROSETOPHYLLOUS DESERT SHRUBLAND								
Amaranthaceae								
Atriplex canescens (Pursh) Nutt.	12	48	1.28	3	1.24	20.39	0.23	0.92
Asparagaceae								
Agave americana L.	35	140	3.74	9	3.72	53.53	0.61	2.69
Agave lecheguilla Torr.	251	1004	26.82	20	8.26	7550.69	86.69	40.59
Agave striata Zucc.	24	96	2.56	4	1.65	53.65	0.62	1.61
Dasylirion texanum Scheele	22	88	2.35	7	2.89	51.80	0.59	1.95
Yucca filifera Chabaud	1	4	0.11	1	0.41	0.38	0.00	0.17
Asteraceae								
Artemisia ludoviciana Nutt.	7	28	0.75	1	0.41	10.64	0.12	0.43
Gutierrezia microcephala (DC.) A. Gray	52	208	5.56	8	3.31	30.67	0.35	3.07
Gymnosperma glutinosum (Spreng.) Less.	1	4	0.11	1	0.41	2.83	0.03	0.18
Parthenium incanum Kunth	3	12	0.32	1	0.41	3.94	0.05	0.26
Viguiera stenoloba S.F.Blake	15	60	1.60	1	0.41	26.74	0.31	0.77
Berberidaceae								
*Berberis trifoliolata*Moric.	16	64	1.71	7	2.89	23.71	0.27	1.62
Cactaceae								
Coryphantha compacta (Engelm.) Orcutt	1	4	0.11	1	0.41	0.02	0.00	0.17
Coryphantha difficilis (Quehl) Orcutt	6	24	0.64	4	1.65	0.06	0.00	0.76
Coryphantha neglecta L. Bremer	18	72	1.92	6	2.48	0.82	0.01	1.47
Cylindropuntia imbricata (Haw.) F.M.Knuth	1	4	0.11	1	0.41	1.13	0.01	0.18
Cylindropuntia leptocaulis (DC.) F.M. Knuth	23	92	2.46	9	3.72	45.56	0.52	2.23
Echinocactus horizonthalonius Lem.	5	20	0.53	3	1.24	0.27	0.00	0.59
Echinocereus enneacanthus Engelm.	12	48	1.28	3	1.24	1.90	0.02	0.85
Echinocereus pectinatus (Scheidw.) Engelm.	22	88	2.35	9	3.72	0.47	0.01	2.02
Echinocereus stramineus (Engelm.) F.Seitz	2	8	0.21	1	0.41	1.69	0.02	0.22
Ferocactus hamatacanthus (Muehlenpf.) Britton & Rose	2	8	0.21	1	0.41	0.25	0.00	0.21
Lophophora williamsii (Lem. ex Salm-Dyck) J.M. Coult.	23	92	2.46	6	2.48	0.35	0.00	1.65
Mammillaria melanocentra Poselger	1	4	0.11	1	0.41	0.05	0.00	0.17
Mammillaria pottsii Scheer ex Salm-Dyck	42	168	4.49	8	3.31	0.55	0.01	2.60
Neolloydia conoidea (DC.) Britton & Rose	1	4	0.11	1	0.41	0.01	0.00	0.17
Opuntia engelmannii Salm-Dyck ex Engelm.	7	28	0.75	5	2.07	4.38	0.05	0.95
Sclerocactus scheeri (Salm-Dyck) N.P. Taylor	3	12	0.32	2	0.83	0.09	0.00	0.38
Thelocactus bicolor (Galeotti ex Pfeiff.) Britton & Rose	5	20	0.53	2	0.83	0.08	0.00	0.45
Celastraceae								
Mortonia greggii A. Gray	33	132	3.53	8	3.31	64.68	0.74	2.52
Ephedraceae								
Ephedra antisyphilitica Berland. ex C.A. Mey.	4	16	0.43	3	1.24	6.90	0.08	0.58
Euphorbiaceae								
Bernardia myricifolia (Scheele) S. Watson	6	24	0.64	3	1.24	12.70	0.15	0.68
Jatropha dioica Cerv.	18	72	1.92	5	2.07	36.30	0.42	1.47
Fabaceace								
Acacia berlandieri Benth.	31	124	3.31	12	4.96	69.09	0.79	3.02
Acacia greggii A. Gray	23	92	2.46	11	4.55	21.44	0.25	2.42
Calliandra conferta Benth.	35	140	3.74	8	3.31	129.52	1.49	2.84
Eysenhardtia texana Scheele	2	8	0.21	1	0.41	12.58	0.14	0.26
Prosopis glandulosa Torr.	22	88	2.35	9	3.72	113.21	1.30	2.46
Sophora secundiflora (Ortega) Lag. ex DC.	12	48	1.28	3	1.24	49.31	0.57	1.03
Koeberliniaceae								
Koeberlinia spinosa Zucc.	1	4	0.11	1	0.41	7.54	0.09	0.20
Oleaceae								
Forestiera angustifolia Torr.	3	12	0.32	3	1.24	8.80	0.10	0.55
Pinaceae								
Pinus catarinae Passiini	6	24	0.64	4	1.65	31.53	0.36	0.89

Table 2. (continued)

Species	No.	Abundance (N/ha) Absolute	Relative	Frequency Absolute	Dominance (m^2-ha) Relative	Absolute	Relative	RIV (%)
Rhamnaceae								
Karwinskia humboldtiana (Schult.) Zucc.	4	16	0.43	3	1.24	14.96	0.17	0.61
Condalia hookeri M.C. Johnst.	17	68	1.82	8	3.31	49.79	0.57	1.90
Scrophulariaceae								
Leucophyllum frutescens (Berland.) I.M. Johnst.	30	120	3.21	11	4.55	29.80	0.34	2.70
Ulmaceae								
Celtis pallida Torr.	1	4	0.11	1	0.41	8.55	0.10	0.21
Zygophyllaceae								
Guaiacum angustifolium Engelm.	47	188	5.02	11	4.55	61.38	0.70	3.42
Larrea tridentata (Sessé & Moc. ex DC.) Coville	28	112	2.99	11	4.55	95.76	1.10	2.88
Total	**936**	**3744**	**100.00**	**242**	**100.00**	**8710.46**	**100.00**	**100.00**

et al. (2013) recorded *Cordia boissieri* as part of the community but not as the most abundant. They recorded *Diospyros texana* instead, as the most abundant species for communities located in Linares, Nuevo Leon. Furthermore Foroughbakch et al. (2013) recorded *Prosopis glandulosa* as most abundant. The studied community presented geographic affinity with the medium semithorn shrubland the Altiplano and the Coastal Plain, to have associations of *Cordia-Leucophyllum-Zanthoxylum*, although the genus *Zanthoxylum* is not predominant in previous studies (Briones & Villarreal 2001). According to Muller (1947), the lower elevation and greater precipitation correlate with vegetation characterized by thorny species and a growth more dense of shrubs and low trees.

Fabaceae was the best represented family of the semithorn shrubland community with 10 species, which is consistent with the findings of Estrada et al. (2005), who in turn reported to *Acacia rigidula* as the characteristic species of this community as well as species such as *Acacia berlandieri* and *Havardia pallens*. For the present study, *A. rigidula* was also abundant, but species like *A. berlandieri* and *H. pallens* were not. The most common species was *Cordia boissieri*, which according to Garcia and Jurado (2008) is characteristic of semithorn shrubland communities. High abundance of *Leucophyllum frutescens* is also registered. This association *Acacia-Leucophyllum-Cordia* has been registered by Rojas (1965) as community characteristic of the Coastal Plain of Northeast Mexico; Briones and Villarreal (2001) reported similar associations in an ecotone between the provinces of the Altiplano and Coastal Plain of northeast Mexico. This association is mainly due to humid conditions where the development of these species is favorable. This humidity is carried by winds from the sea of the Gulf of Mexico and is intercepted in the foothills of the Sierra Madre Oriental at the altitude of the community studied (850 m a.s.l.; Briones & Villarreal 2001).

The most representative family of the piedmont scrub community was Fabaceae, with 9 species. This family has been reported as the most representative in the region (Garcia & Jurado 2008; Canizales et al. 2009; Estrada et al. 2012; Mata et al. 2014).. The most abundant species recorded in this study was *A. rigidula*; this agrees with Canizales et al. (2009) who recorded *A. rigidula* as the most abundant species. This study differs from that found by Garcia and Jurado (2008) and Estrada et al. (2012), who studied an area with non-disturbance appearance with a high presence of *Helietta parvifolia*. In contrast, Mata et al. (2014) reported a high abundance of *A. lecheguilla*, an element that is not recognized as abundant within this community because the area sampled was altered by anthropogenic activities.

The most representative family of the rosetophyllous desert shrubland was Cactaceae with 16 species. The most abundant and frequent species was *A. lecheguilla*, referred by Alanis et al. (1996), Rzedowski (2006), and Mata et al. (2014) as the most characteristic species within of this community in the northeastern Mexico.

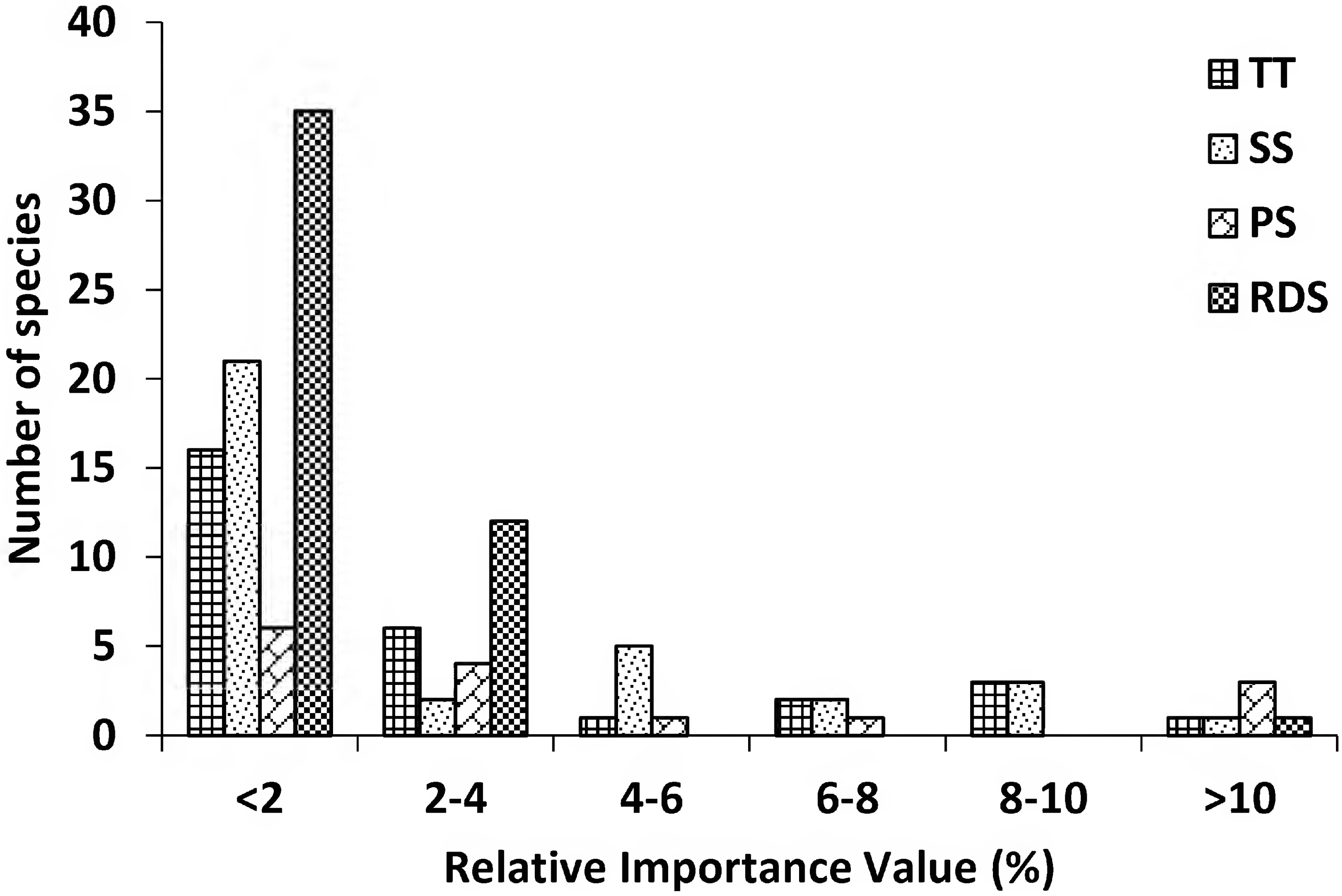

Fig. 2. Frequency distribution of *RIV* in the communities assessed: **TT**, tamaulipan thornscrub; **SS**, semithorn shrubland; **PS**, piedmont scrub; **RDS**, rosetophyllous desert shrubland.

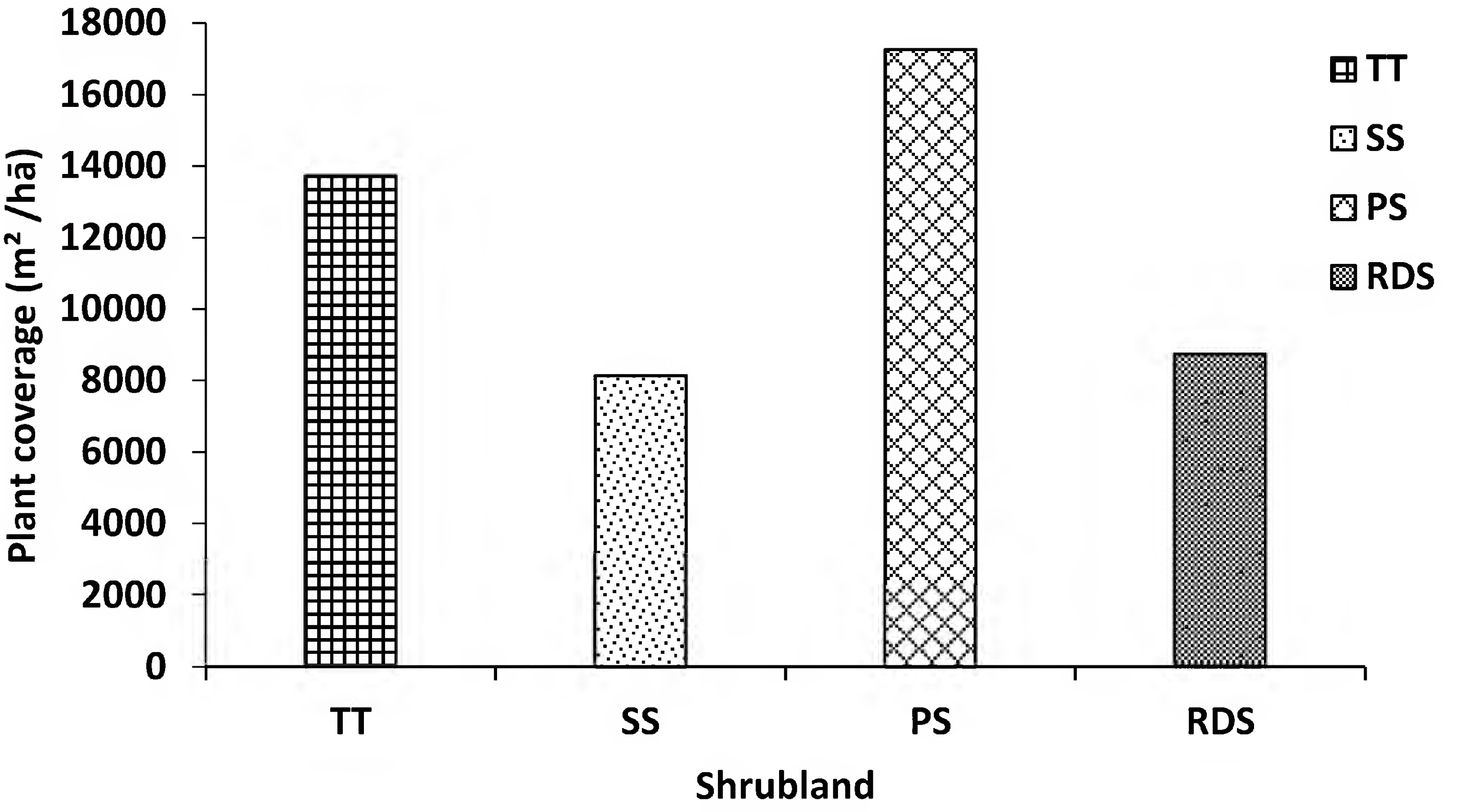

Fig. 3. Plant coverage of the communities assessed: **TT**, tamaulipan thornscrub; **SS**, semithorn shrubland; **PS**, piedmont scrub; **RDS**, rosetophyllous desert shrubland.

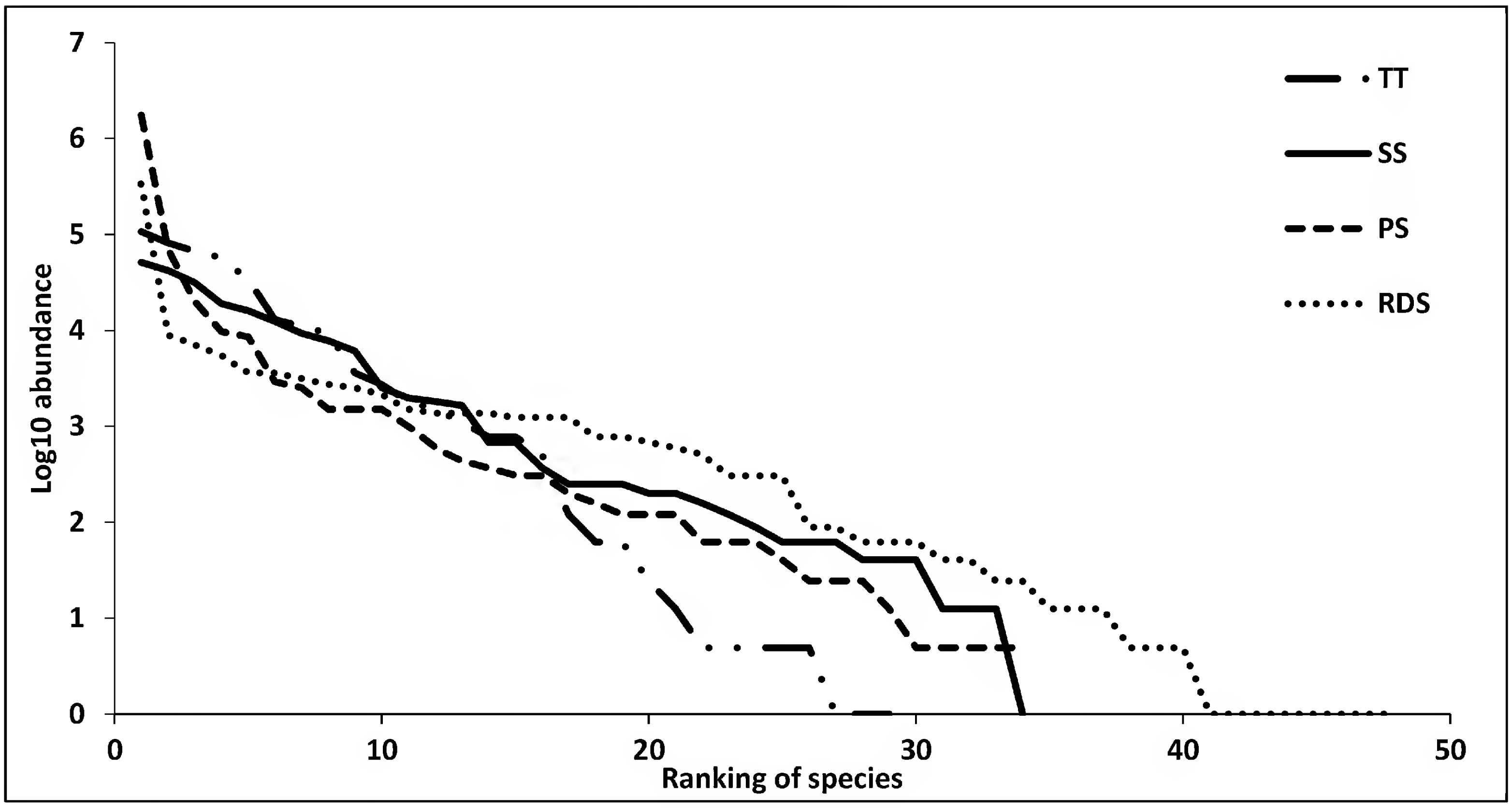

Fig. 4. Dominance-diversity of species curve.

Relative importance Value (RIV).—Distribution of frequencies in the four regions showed that the number of species with low ecological weight was greater than the number of species with high ecological weight. This was most evident in the RDS community which presented 35 species with an importance value index < 2%, which indicated a high diversity in this community where there is no high dominance of any large number of species. The species that stands out with respect to its *RIV* was *A. lecheguilla* (40.59%), a result consistent with that found for a community on the border between the states of Nuevo Leon and Coahuila (Mata et al. 2014) which recorded as having the highest value of *RIV* for this species. Following this community is SS and TT with 21 and 16 species, respectively. *Cordia boissieri* had the highest *RIV* within the TT and SS communities (19.25% and 10.37% respectively). However, other studies have reported *A. rigidula* as a species with a high value of importance (Estrada et al. 2004; Gonzalez et al. 2010). Furthermore, Alanis et al. (2008) reported *A. rigidula* as the most prevalent species in areas with a history of agriculture, livestock, and clear cutting. Jimenez et al. (2009) also reported *A. rigidula* as the species of greatest ecological value for a clear cutting area in Linares, while Mora et al. (2013) recorded *Diospyros texana*, *Prosopis laevigata,* and *A. farnesiana* with the highest *RIVI* values for TT, in livestock areas, regeneration areas, and reference areas, respectively. Moreover, Jimenez et al. (2009, 2012) noted a case of *D. texana* growing in an area with a history of agriculture. The high presence of *A. rigidula* in areas with a history of agricultural use is because it is identified as an important component of the diet of small grazing ruminants (Ramirez 2009). In the present study, the TT community did not have a history of such use.

The lowest number of species was found in the piedmont scrub community (6 species). Nevertheless, it is the best represented category which is consistent with studies reporting 3 species with the highest *RIV* values (Canizales et al. 2009; Mata et al. 2014) as in the present work. However, the species were different between studies, coinciding only in the genus *Acacia*, which can be due to a different usage history in the presented areas. Meanwhile, Garcia and Jurado (2008) reported *Helietta parvifolia* as a species with the highest *RIV* (52.14%) which was supported by the work of Estrada et al. (2012). This information differs from that found by the present study because this species was not found in the sampled community, and piedmont scrub communities have undergone structural changes over time, which has brought a change in composition and structure as noted by Canizales et al. (2009). These authors reported a low abundance attributed to the history of extensive use which has reduced their populations to small groups in isolated communities which are largely undisturbed (Garcia & Jurado 2008; Canizales et al. 2009).

Plant coverage.—The greatest coverage was recorded in the piedmont scrub community (17,267.78 m^2/ha), which was higher than that found by Canizales et al. (2009) at 9,724.27 m^2/ha. Also, Mata et al. (2014) reported the greatest coverage for a community of PS along the border of Nuevo Leon and Coahuila, while for the rosetophyllous desert shrubland the same authors reported a lower coverage (1,716 m^2/ha) than that of the present study. The semithorn shrubland (SS) had the lowest coverage (8,138.43 m^2/ha) of the communities studied composed predominantly of low-growing species such as *Leucophyllum frutescens* and *Croton torreyanus*. Following the SS community was the rosetophyllous desert shrubland (8,710.46 m^2/ha) where predominate life forms are rosettes and succulents.

The community with the second highest coverage was Tamaulipan thornscrub (TT), with 13,718.68 m^2/ha. Lower coverage for areas of shrubland, regeneration, and livestock in the southern Nuevo Leon were recorded by Mora et al. (2013).

Distribution of abundance of species.—Distribution of species with respect to their proportional abundance demonstrated that species follow a normal distribution, since many species have intermediate values of either very low or very high abundance (Martella et al. 2012), where these species are distributed towards the tails of the distribution curve (Aguirre et al. 2008). This type of distribution is reported in northeastern Mexico in plant communities at mature successional stage (Molina et al. 2014).

In conclusion, the results from this research lead us to note that there are constant changes in the species composition of these plant communities. Therefore it is important to develop strategies to conserve these ecosystems as well as develop a sustainable management program.

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BOOK NOTICE

Mohamed A.F. Noor. 2012. **You're Hired! Now What? A Guide for New Science Faculty.** (ISBN-13: 978-0-87893-963-3, pbk). Sinauer Associates, Inc., Publishers, 23 Plumtree Road, P.O. Box 407, Sunderland, Massachusetts 01375-0407, U.S.A. (**Orders:** www.sinauer.com, 1-413-549-4300). $14.41 US, 96 pp., 1 illustration, 6" × 9".

From the publisher: You're Hired! Now What? is a short, conversationally written handbook describing challenges and specific strategies to get ahead (or at least get by) in an academic setting. New college faculty are well-versed in the scientific skills they'll need for success in research, including design of projects, preparation of manuscripts and grant proposals, and interactions during peer review. Yet typically they receive no training in organization, management, or even basic college structure. This book is an attempt to begin to fill this void, presenting thoughts and advice intended as a starting point for thinking about problems faced by new faculty.

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MATELEA CHIHUAHUENSIS (APOCYNACEAE): AN ADDITION TO THE FLORA OF THE UNITED STATES AND A SYNOPSIS OF THE SPECIES

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ABSTRACT

Matelea chihuahuensis is reported as an addition to the floras of New Mexico and the United States with three occurrences in close proximity documented from Hidalgo County. A full description of the species is presented, along with photos, a distribution map, and a review of its taxonomic history. A lectotype is designated. *Matelea chihuahuensis* is compared to its close relatives and a key is provided to aid in distinguishing similar *Matelea* species in Chihuahua.

RESUMEN

Matelea chihuahuensis se reporta como una adición a las floras de Nuevo México y Estados Unidos con tres ocurrencias en las proximidades de las documentadas en el condado de Hidalgo. Se presenta una descripción completa de la especie, junto con fotos, un mapa de la distribución, y una revisión de su historia taxonómica. Se designa un lectotipo. *Matelea chihuahuensis* se compara con sus parientes cercanos y se proporciona una clave para ayudar a distinguir las especies *Matelea* similares en Chihuahua.

Key Words: Apocynaceae, *Matelea*, Milkweed, North American Flora, Noteworthy Collection

INTRODUCTION

The Sky Island region of the southwestern United States and northwestern Mexico is a biologically diverse area that is an ongoing source of botanical novelties. The Madrean 'islands' describe an archipelago of mountains clad with evergreen oak and coniferous forests, interspersed with valleys of grasslands and scrub, and which connect the Sierra Madre Occidental and the Rocky Mountain cordilleras (Warshall 1994). Some species with widespread ranges in Mexico, in the Sierra Madre Occidental or beyond, have long been known to occur in the U.S. from only one or a few sites in southeastern Arizona, e.g., *Henrya insularis* Nees (Acanthaceae; Daniel 2004), *Cynanchum ligulatum* (Benth.) Woodson (Apocynaceae; Sundell 1993), *Dichondra sericea* Sw. (Convolvulaceae; Austin 2006), *Coursetia glabella* (A. Gray) Lavin (Fabaceae; Lavin 1988), and *Quercus viminea* Trel. (Fagaceae; Van Devender et al. 2013). Among these are species that have never been re-collected following their initial discovery in the U.S., e.g., *Pherotrichis schaffneri* A. Gray (Apocynaceae) and *Diphysa thurberi* (A. Gray) Rydb. ex Standl. (Fabaceae) (Kearney & Peebles 1961). Such discoveries continue in the region: *Mandevilla foliosa* (Müll. Arg.) Hemsl. (Apocynaceae; Milsom & Chamberland 2013) and *Echinochloa oplismenoides* (E. Fourn.) Hitchc. (Poaceae; Fishbein 1995) were reported as new to the United States and *Eriogonum terrenatum* Reveal (Polygonaceae; Reveal 2004) was described as a new species. Similar to those discoveries in Arizona, the smaller part of the Sky Island region in southwestern New Mexico recently has seen the discovery of a species new to the U.S., *Grindelia oxylepis* Greene (Asteraceae; Spellenberg 2014), and another new to science, *Euphorbia rayturneri* V.W. Steinm. & Jercinovic (Euphorbiaceae; Steinmann & Jercinovic 2013). To this list of novelties in the New Mexico portion of the Sky Island region we add *Matelea chihuahuensis* (A. Gray) Woodson

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(Apocynaceae). To our knowledge, there is no common name for this species, but we recommend using Chihuahuan hairy milkvine.

Matelea Aubl. is a genus of approximately 225 species in Apocynaceae subfamily Asclepiadoideae. While vines are the predominant growth form in *Matelea*, other growth forms occur as apparent adaptations to grassland and woodland environments. In the southern United States and northern Mexico, several *Matelea* species are prostrate to decumbent, non-twining herbs. These species appear to be most closely related to *Pherotrichis* Decne., a genus segregated from *Matelea* and characterized by an erect, non-twining habit, as well as several species of microphyllous to moderately small-leaved vines, such as *M. parvifolia* (Torr.) Woodson and *M. producta* (Torr.) Woodson (Krings et al. 2008; Parks 2008). Together, this group of ~30 arid-adapted species corresponds loosely with Woodson's (1941) *Matelea* subg. *Chthamalia* (Decne.) Woodson, which is under revisionary study by A. McDonnell (unpubl. data), and which includes the poorly known species *Matelea chihuahuensis* (Fig. 1).

The type specimen of *Matelea chihuahuensis* was collected by Cyrus Guernsey Pringle during the early part of the period during which he completed his most well known work: exploration and collection of plant specimens throughout Mexico from 1885 to 1909 (Davis 1936; Knobloch 1979; Stafleu & Cowan 1983; Mauz 2011). The specimens were divided into numerous sets distributed to the major herbaria of the time, including one sent to Harvard University. There, Asa Gray described many new species from Pringle's specimens. Gray described *M. chihuahuensis* as a species of *Gonolobus* Michx., where nearly all North American milkweed vines of subtribe Gonolobinae were placed at the time. As syntypes of *G. chihuahuensis* A. Gray, he cited Pringle's collections #104 (with flowers, 1885) and #692 (with flowers and fruits, 22 August 1885) gathered from the hills around Chihuahua. In his journal, Pringle describes the circumstances surrounding the collection of #692. In the prior days, he had returned from the Santa Eulalia Mountains to collect in "the valley toward Nombre de Dios" and the nearby cliffs (Davis 1936, p. 26). His #692 was collected "out around the railroad shops" and must be from the area now part of the east side of Chihuahua City that has engulfed Nombre de Dios, the site of caves that are presently a tourist attraction. A freight railroad still parallels Federal Highway 45 in this area.

Gray described *Gonolobus chihuahuensis* as procumbent, spreading, hairy on all sides, and with many stems and leaves. He noted that the new species shared these characters with two other prostrate milkweeds known to him, *Matelea parviflora* (Torr.) Woodson (of Texas) and *M. pedunculata* (Decne.) Woodson (of Michoacán and adjoining states). He highlighted the floral differences between this species and all others known at the time: "the crown [corona] is perfectly simple, with no internal crests or appendages, the margin abruptly produced into the five narrow and entire lobes which overtop the anthers, these of the firm texture which is common in the *Chthamalia* section, of which this species has wholly the aspect." (Gray 1886). Thus, he hypothesized a close alliance with *Chthamalia* Decne., (Decaisne 1844). However, Gray did not recognize *Chthamalia* as a genus distinct from *Gonolobus* (Engelmann & Gray 1845; McDonnell 2014).

When Woodson (1941) revised the circumscription of *Matelea*, reducing many formerly recognized genera to subgenera, he did not place *M. chihuahuensis* in *Matelea* subg. *Chthamalia,* but rather in *Matelea* subg. *Pherotrichis* (Decne.) Woodson. Based on his key to the subgenera (1941), subg. *Chthamalia,* is distinct in having "subquadrate to oblong-reniform pollinia with a narrow hyaline margin" while subg. *Pherotrichis* has "falciform or arcuate pollinia with no hyaline margin." In contrast to the pollinia characteristics highlighted by Woodson, the vegetative morphology, flowers, and fruits of *M. chihuahuensis* accord much more closely with the prostrate species placed by Woodson in subgenus *Chthamalia* than with the erect herbs he placed in subgenus *Pherotrichis.* As noted above, phylogenetic studies have shown that species in these subgenera are close relatives (Krings et al. 2008; Parks 2008). Further study is required to revise generic circumscriptions and definitively place *M. chihuahuensis.*

The species of subg. *Chthamalia* that share the prostrate to ascending habit of *Matelea chihuahuensis* are distributed from the southern U.S. to south-central Mexico. The most widespread species are *M. biflora* (Nutt. ex Raf.) Woodson and *M. cynanchoides* (Engelm. & A. Gray) Woodson of the south-central U.S. (McDonnell

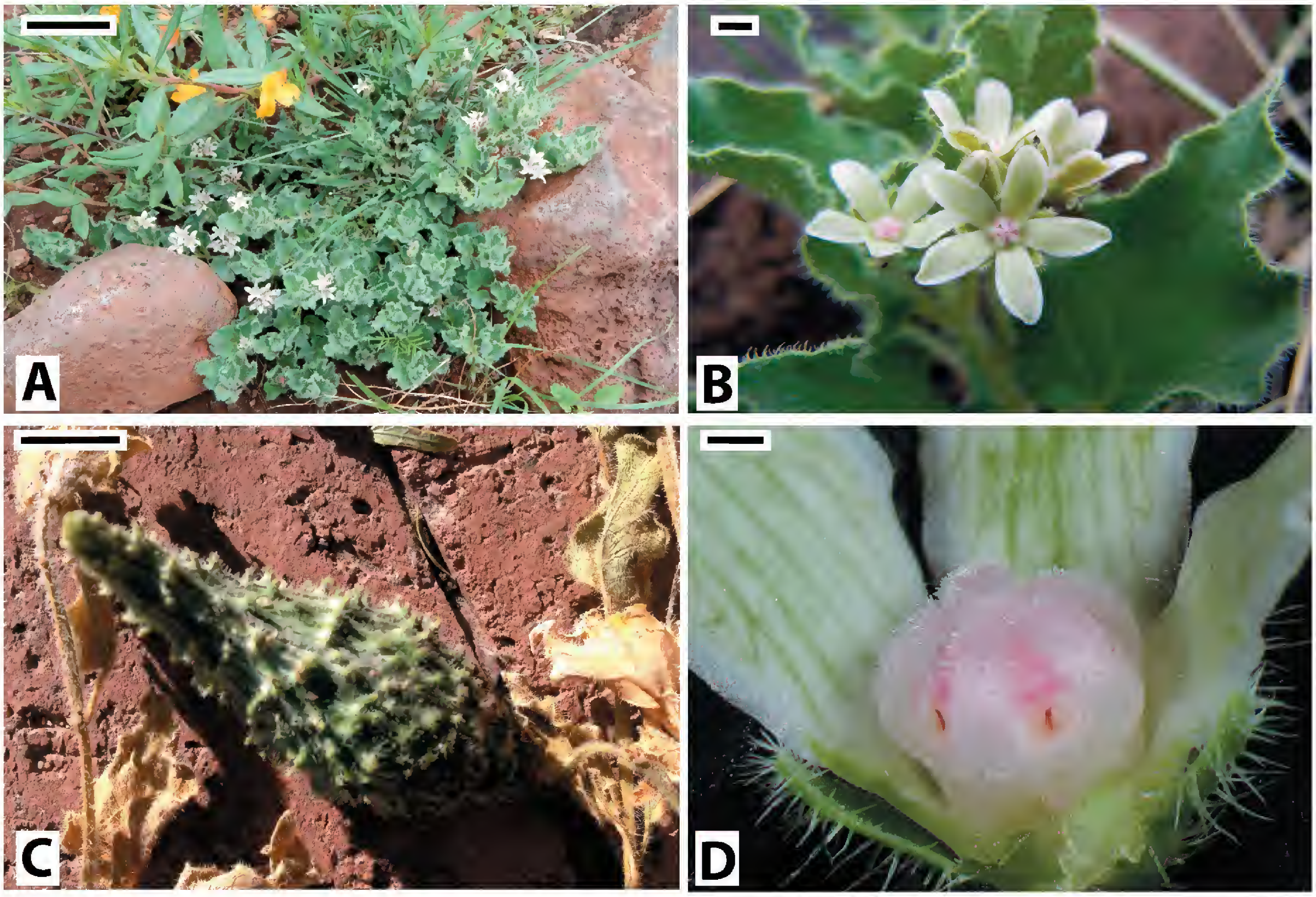


Fig. 1. ***Matelea chihuahuensis*** **A.** **Habit, scale = 5 cm.** **B.** **Inflorescence, scale = 1 mm.** **C.** **Follicle, scale = 1 cm.** **D.** **Detail of flower, with 2 petals removed, scale = 0.5 mm.**

2014) and *M. pedunculata* of southwestern Mexico. The remaining species in the subgenus have narrow ranges, including three species that until now were considered to be endemic to Chihuahua, Mexico. These are *M. chihuahuensis*, *M. lesueurii* (Standl.) Woodson, and *M. wootonii* (Vail) Woodson, each of which is documented by a small number of collections. Many of these collections have remained unidentified, occasionally others have been misidentified, and in the latter situation it is not unusual for the specimens to be identified as *M. chihuahuensis*. For example, a vegetative specimen from Laguna Babicora (*Lebgue & Estrada 3206a* [NMC]) was collected and cited as *M. chihuahuensis* (Estrada-Castillón et al. 1997) but is actually *M. lesueurii* (see also *McDonnell 227* [OKLA] from the same locality). We provide here the first detailed morphological description of *M. chihuahuensis* and document this species as a new member of the flora of the United States. We also provide a key to distinguish this species from similar species in Chihuahua.

MATERIALS AND METHODS

Locality information was downloaded from online specimen repositories (including the Global Biodiversity Information Facility: GBIF; www.gbif.org, TROPICOS: tropicos.org, and SEINet: http://swbiodiversity.org/portal/index.php) and/or obtained directly from specimen labels. Specimen loans and images were obtained from the Botanical Research Institute of Texas (BRIT), the California Academy of Sciences (CAS), Michigan State University (MSC), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), Harvard University (GH/HUH), the Rancho Santa Ana Botanic Garden (RSA/POM), University of Texas at Austin (TEX/LL), the Smithsonian Institution (US), and JSTOR Global Plants (plants.jstor.org/). Herbarium abbreviations follow Thiers (2014). Occurrence data were georeferenced using Google Earth (build 7.1.2.2041, 7 Oct 2013). New specimens were obtained through fieldwork in the states of New Mexico and Chihuahua. A distribution map was produced using ArcGIS® ArcMap™ v.10.2 (Esri, Redlands, CA) and Adobe® Illustrator CS4

(Adobe Systems Inc., San Jose, CA). Due to imprecise locality data of some older specimens, two of the 14 records for *M. chihuahuensis* were excluded from the map. Measurements of floral and vegetative characters were made from herbarium specimens as well as from fresh and liquid-preserved flowers using Olympus® cellSens Entry 1.6 imaging software and an Olympus® SZX10 dissecting microscope outfitted with an Olympus® SC30 CMOS color camera. Measurements of digital specimen images were made using ImageJ software 1.48v (Rasband 1997–2014).

RESULTS AND DISCUSSION

Previous collections of *Matelea chihuahuensis* document a sparse but widespread distribution in Chihuahua (Fig. 2). It has been collected several times in the vicinity of Chihuahua City (*Pringle 104*, *692*, *880*; *Palmer 214*; *Freytag & Baxter 6*; *LeSueur 1182*). It has also been found further west and northwest of the city in the foothills of the Sierra Madre Occidental, near San Diego del Monte (*Hartman 735*), and Colonia Juárez (*Jones s.n.*; *Pennell 19072*). One collection was made at a disjunct site in the main cordillera of the Sierra Madre, at Mesa de Basaseachic (*LeSueur 2009*). This location is considered suspect given the more eastern and seemingly more arid habitats of all other collection sites. The species has also been documented at disjunct locations in desert mountains in far northeastern Chihuahua, south of Pirámide (*Johnston 8104*) and in the Sierra Hechiceros (*Stewart 220*). Fieldwork conducted by A. McDonnell and M. Fishbein of Oklahoma State University and S. González Elizondo and L. Ruacho González of Centro Interdisciplinario de Investigación para el Desarollo Integral Regional Unidad Durango, Instituto Politécnico Nacional, was successful in locating a new Chihuahuan population in the foothills of an eastern branch of the Sierra Madre, in the Sierra La Catarina (*McDonnell 211*). It is noteworthy that *M. lesueurii* also inhabits these mountains, though at higher elevation and in more mesic grasslands (*McDonnell 203* [CIIDIR, MO, OKLA]).

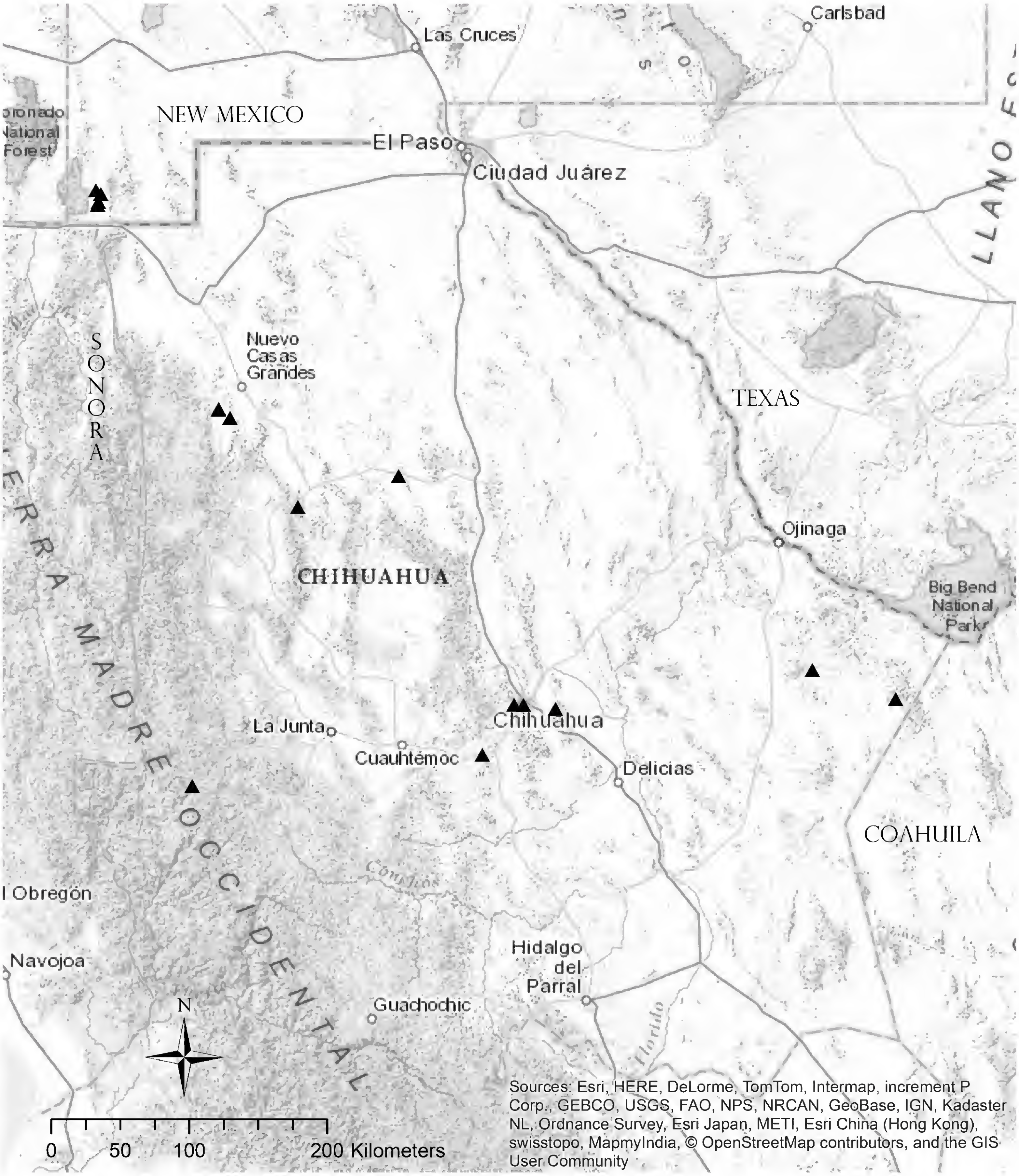
Our research shows that, until now, *Matelea chihuahuensis* has not been documented outside of the state of Chihuahua (Vega-Mares et al. 2014). However, during vegetation surveys in the fall of 2013, three new locations were found in close proximity (≤ 8 km) of each other on the Diamond A Ranch (formerly Gray Ranch), in the bootheel of New Mexico (*Quinn s.n.*). These plants were either non-reproductive or in fruit. Photos and a specimen including viable seeds were sent to M. Fishbein and A. McDonnell for identification. Plants grown from seed in January 2014 flowered approximately five months after germination and were positively identified as *Matelea chihuahuensis* (*McDonnell 199*). The individuals from New Mexico represent the northernmost and westernmost stations for this species and are additions to the floras of New Mexico and the United States.

Though there are relatively few collections of this species, we believe it to be most common on rocky substrates in drier grasslands and pastures in foothills of the eastern slope of the Sierra Madre Occidental. In Chihuahua, we found *Matelea chihuahuensis* (*McDonnell 211*) growing in the Sierra La Catarina on a moderate, rocky slope in grassland dominated by *Bouteloua* spp. with scattered *Cylindropuntia imbricata* (Haw.) F.M. Knuth, *Dasylirion wheeleri* S. Watson ex Rothr., *Fouquieiria splendens* Engelm., *Aloysia gratissima* (Gillies & Hook.) Tronc., and *Mimosa biuncifera* Benth. We were not able to locate historically documented populations at several sites we visited in Chihuahua, including one northeast of the Sierra La Catarina (*Yen & Estrada 7224*) where the vegetation was described as "matorral microfilo" on the specimen label. The vegetation at this site was dominated by *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger, *Prosopis glandulosa* Torr., *Mimosa biuncifera*, and *Aloysia gratissima*, suggesting the species occurs at least occasionally in desertscrub. The New Mexican populations were found in *Bouteloua*-dominated grassland, in sandy loam overlying clay, on the western piedmont of the Animas Mountains.

Matelea chihuahuensis perennates from a thickened taproot and its phenology is likely correlated with patterns of rainfall. Most flowering specimens have been collected in July and August following the onset of summer rains. Fruiting specimens have been collected between the months of July and October. Pollinators or other fauna that might interact with *M. chihuahuensis* are unknown.

Closely Related Species

Occasionally, collectors have confused closely related species for *Matelea chihuahuensis*. Prostrate species of


Carlsbad
Las Cruces
NEW MEXICO
Coronado National Forest
El Paso
Ciudad Juárez
LLANO
Nuevo Casas Grandes
SONORA
TEXAS
SIERRA MADRE OCCIDENTAL
CHIHUAHUA
Ojinaga
Big Bend National Park
La Junta
Chihuahua
Cuauhtémoc
Delicias
COAHUILA
Obregón
Navojoa
Hidalgo del Parral
Guachochic
N
0 50 100 200 Kilometers

Sources: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Fig. 2. Distribution of *Matelea chihuahuensis* in Chihuahua, Mexico, and New Mexico, USA. Collection sites illustrated with black triangles.

Matelea have a similar overall appearance, including multiple stems and cordate to orbicular leaves. However, the species are difficult to confuse in flower—*M. chihuahuensis* is especially distinct with cream and green-striate corollas and pilose, terete, translucent-white corona segments that overtop the anthers (vs. purplish to maroon corollas with white to maroon coronas). *Matelea chihuahuensis* can be distinguished from similar Chihuahuan species by herbage that is densely hirsute throughout and leaves with undulate margins that provide a ruffled appearance to the blades. *Matelea lesueurii* differs by having suborbicular leaves that are glabrous and shiny adaxially and densely hirsute abaxially, the margins entire and planar. *Matelea wootonii* also has suborbicular leaves with glabrous adaxial surfaces, sparsely hirsute abaxial surfaces and entire, planar margins. These species can be distinguished with the key presented below. All three species are found in the state of Chihuahua; *M. lesueurii* and *M. wootonii* generally grow at higher elevations and in more mesic habitats than does *M. chihuahuensis*.

Other prostrate or procumbent species similar to *Matelea chihuahuensis* occur outside of Chihuahua. In southern Texas, Coahuila, and Tamaulipas, two to three species occur: *M. brevicoronata* (B.L. Rob.) Woodson, *M.* aff. *brevicoronata*, and *M. parviflora*. To the south of Chihuahua, *Matelea* aff. *pedunculata* (Decne.) Woodson occurs in Durango and Zacatecas. All of these taxa share with *M. chihuahuensis* the dense vestiture of trichomes and undulate leaf margins. Vegetatively, these species are difficult to distinguish, but in flower they are rather distinct. While *M. chihuahuensis* has a green and white corolla, both *M. brevicoronata* and *M. parviflora* have more or less uniformly bright green corollas with little or no white in them and *M.* aff. *brevicoronata* has a green corolla when young that becomes maroon with age. At maturity, the corolla lobes of *M. parviflora* are reflexed and in *M. brevicoronata* they are campanulate. In both *M. chihuahuensis* and *M.* aff. *brevicoronata*, the corollas are rotate, but the species differ in color as noted above. The species that occur in Texas all have strap-shaped corona segments that vary in length but are not translucent and do not arch over the anthers as they do in *M. chihuahuensis*. One specimen collected 8 miles south of Mirando City in Webb County, Texas (*Turner 80-61* [TEX]), was originally identified as *M. chihuahuensis*, but has been confirmed to be *M. parviflora*. *M.* aff. *pedunculata* differs conspicuously from *M. chihuahuensis* by having tubular-campanulate corollas that are muted green-brown with maroon striations. Its corona is much shorter, yellowish in color, and does not overtop the anthers.

TAXONOMIC TREATMENT

Matelea chihuahuensis (A. Gray) Woodson, Ann. Missouri Bot. Gard. 28:232. 1941. *Gonolobus chihuahuensis* A. Gray. Proc. Amer. Acad. Arts 12:398–399. 1886. Type: MEXICO. Chihuahua: rocky hills near Chihuahua, 22 Aug 1885, *C.G. Pringle 692* (lectotype, designated here, GH; isolectotypes, AC digital image, BR digital image, CAS, CORD digital image, E digital image, F, G, 2 sheets-digital images, GOET digital image, JE digital image, MICH digital image, NY, 3 sheets, RSA digital image, US, 2 sheets).

Plants: perennial, prostrate to procumbent, malodorous and hispid-hirsute throughout, usually with 5–20+ stems from a thickened taproot, stem length in flower 10–50 cm, lengthening in fruit. **Leaves:** largest with petioles 0.2–1.6 cm long, blades deltoid to cordate, occasionally ovate, 0.7–3.3 cm long and 0.7–2.6 cm wide, bases deeply to shallowly cordate, apices acute, margins undulate; leaf bases with 2–4 narrowly conical colleters that may break off on mature leaves. **Inflorescences:** axillary umbels of 2-5 flowers; peduncles 1-3 cm long. **Flowers:** pedicels 3.5-5.0 mm; calyx lobes 5, elliptic, 1.9–3.5 mm long; corolla aestivation contorted, after expansion shallowly campanulate-rotate, cream to white with fine green striations on adaxial surfaces, green and white with green striations on abaxial surfaces, 3.8–7.9 mm in diameter, deeply 5-lobed; the lobes oblong to spathulate, hirsute at base adaxially, glabrous abaxially, margins planar; corona consisting of 5 basally-united lobes, arising at the junction of the gynostegial column and the corolla, incurved, incumbent on apex of anthers and style, strap-like, approximately elliptic in cross section, densely hirsute, translucent cream to white; style apex white with pink striations visible through corona. **Fruit:** follicle, muricate, ovate to lanceolate or elliptic with an acuminate apex, green with dull green striations, 4.94–5.7 cm long, 1.7–2.4 cm wide, protuberances numerous, 0.06–1.6 mm in height.

Specimens examined.—**MEXICO. CHIHUAHUA. Mpio. de Buenaventura:** Carretera Sueco-Flores Magón, 5–6 km, 7 Jul 1997, *C. Yen & E. Estrada 7224* (BRIT); Sierra La Catarina, east slope, about 14 km SW of San Buenaventura, 7 Aug 2014, *A. McDonnell 211* (CIIDIR, MO, OKLA). **Mpio. de Casas Grandes:** plains near San Diego, ~5 mi S of Casas Grandes, 4 Aug 1891, *C.V. Hartman 735* (GH); Colonia Juárez, 11 Sep 1903, *M.E. Jones s.n.* (POM); Colonia Juárez, 21 Sept 1934, *F.W. Pennell 19072* (US). **Mpio. de Chihuahua:** Chihuahua, 1885, *C.G. Pringle 104* (GH); vicinity of Chihuahua, May 1908, *E. Palmer 214* (US); Ray Brown's Canyon, Aug 1936, *H. LeSueur 1182* (F); arroyos 5 mi W of Chihuahua city on Hwy 260, 23 Jul 1975, *G.F. Freytag & J.W. Baxter 6* (GH, MO, US). **Mpio. de Manuel Benavides:** Sierra Hechiceros, 9 km S of Rancho Hechiceros, near the Coahuilan boundary, 1 Oct 1940, *R.M. Stewart 220* (GH). **Mpio. de Ocampo:** Mesa de Basaseachic, 7 Jul 1936, *H. LeSueur 2009* (GH). **Mpio. de Ojinaga:** 7.5 mi S of Pirámide, 11 Aug 1941, *I.M. Johnston 8104* (GH, LL). **U.S.A. NEW MEXICO. Hidalgo Co.:** Gray Ranch (now Diamond A Ranch), rangeland monitoring site plot #5413, Cloverdale Valley, 13 Oct 2013, *M. Quinn s.n.* (OKLA); 11 Jul 2014 *A. McDonnell 199* (OKLA, grown from *Quinn s.n.* seed).

KEY TO THE PROSTRATE SPECIES OF *MATELEA* FOUND IN THE STATE OF CHIHUAHUA, MEXICO

1. Leaves deltoid to cordate, adaxial surface densely hirsute, margins undulate; corolla lobes white with green striations; follicles densely hirsute with 4 or more protuberances per 4 cm length **M. chihuahuensis**
1. Leaves broadly ovate to orbicular, adaxial surface glabrous, margins planar; corolla lobes purple or maroon; follicles very sparsely hirsute with 2 or fewer protuberances per 4 cm length.
    2. Leaves densely hirsute abaxially; margins eciliate **M. lesueurii**
    2. Leaves hirsute only along veins abaxially; margins ciliate **M. wootonii**

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THE FIRST NATURALIZED OCCURRENCE OF THE GENUS *FORSYTHIA* (OLEACEAE) IN ARKANSAS (U.S.A.), WITH ADDITIONAL NOTEWORTHY ANGIOSPERM RECORDS FOR THE STATE

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ABSTRACT

Two species of *Forsythia*: *F. suspensa* (Thunb.) Vahl and *F. viridissima* Lindl., are reported as new for Arkansas. These records represent the first voucher specimen-based documentation of the genus *Forsythia* in the state's flora outside of cultivation. Two additional species of nonnative angiosperms: *Rhodotypos scandens* (Thunb.) Makino and *Trachelospermum jasminoides* (Lindl.) Lem., are documented for only their second occurrences in the state.

RESUMEN

Se citan dos especies de *Forsythia: F. suspensa* (Thunb.) Vahl y *F. viridissima* Lindl., como nuevas para Arkansas. Estas citas representan la primera documentación basada en especímenes testigo del género *Forsythia* en la flora del estado fuera de cultivo. Se documentan dos especies adicionales de angiospermas no nativas: *Rhodotypos scandens* (Thunb.) Makino y *Trachelospermum jasminoides* (Lindl.) Lem., como segundas ocurrencias en el estado.

INTRODUCTION

Forsythia is a genus of about 11 species of deciduous or semi-evergreen shrubs distributed primarily across Asia, with one species in Europe (Chang et al. 1996). Species of *Forsythia* are characterized by opposite, simple (or rarely ternately compound) leaves with entire or coarsely serrate-toothed margins, perfect (bisexual) yellow flowers, often with orange or red-colored nectar guides in the throat that are arranged in solitary or few-flowered axillary inflorescences, and fruits that are small, flattened, few-seeded capsules (Chang et al. 1996). Many species are important as ornamentals in temperate climates for their colorful and profuse display of flowers in early spring, cold hardiness, and ease of cultivation (Bailey and Bailey 1976; Chang et al. 1996).

Two morphologically similar species: *F. suspensa* (Thunb.) Vahl (weeping forsythia) and *F. viridissima* Lindl. (greenstem forsythia), are frequently cultivated in Arkansas, and one or both species have previously been attributed to the Arkansas flora by various sources (Hardin 1974; Thompson 1977; Arkansas Vascular Flora Committee 2006). *Forsythia suspensa* was included in the *Checklist of the Vascular Plants of Arkansas* (Arkansas Vascular Flora Committee 2006), although this record was apparently based on cultivated material (Smith 1988; Gentry et al. 2013). Both species, however, were ultimately excluded from the state's flora because no voucher specimens were available to document the actual occurrence of naturalized plants (Gentry et al. 2013). Consequently, our discovery of *F. suspensa* and *F. viridissima* represents the first verifiable and documented occurrence of these species, along with the genus *Forsythia*, outside of cultivation in Arkansas (Gentry

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et al. 2013). Both species have previously been documented outside of cultivation in the U.S. in several other states (NRCS 2014).

In Arkansas, naturalization and establishment of *Forsythia* species appears to be accomplished primarily vegetatively via air layering of stems, where stems root when in contact with the ground; whole colonies of plants may be produced in this manner. It is important to note, however, that both of the aforementioned species have also been observed in the fruiting condition in Arkansas.

The combination of opposite, coarsely toothed leaves, quadrangular stems with prominent, conical-shaped buds, yellow flowers that are produced in early spring prior to or simultaneously with leaf emergence, and small, flattened, longitudinally furrowed capsules aid in distinguishing species of *Forsythia* from other shrubs in the Arkansas flora.

ADDITIONS TO THE ARKANSAS FLORA

Forsythia suspensa (Thunb.) Vahl (Oleaceae), weeping forsythia (Fig. 1). *Forsythia suspensa* is a deciduous shrub to about 3 m tall that is native to China (Chang et al. 1996). It is naturalized in several states in the eastern U.S. and has also been documented from Kansas, Montana, Utah, and Washington (USDA, NRCS 2014). Some forms of this species, in addition to having simple, unlobed leaves, may exhibit some leaves that are lobed or ternately compound (Krüssmann 1978; Chang et al. 1996).

Voucher specimens: **ARKANSAS. Garland Co.:** a single plant at edge of woods, Entergy Park, Lake Catherine, 16 Sep 2006, *Peck 06-437* (HEND). **Pulaski Co.:** A few plants scattered in disturbed woods, not cultivated, Boyle Park, Little Rock, 11 Mar 2003, *Peck 03011* (HEND).

Forsythia viridissima Lindl. (Oleaceae), greenstem forsythia (Fig. 2). *Forsythia viridissima* is a deciduous to semi-evergreen shrub to about 3 m tall that is native to China (Chang et al. 1996). It is naturalized in several states in the eastern U.S. and has also been documented from Kansas (USDA, NRCS 2014).

Voucher specimens: **ARKANSAS. Clark Co.:** colony of several plants along roadside on slope at edge of disturbed woods, 12th St. ca. one block S of Mill Creek, Arkadelphia, 34.1302778, -093.0611111, 4 Apr 2013, *Serviss 7930* (HEND). **Hot Spring Co.:** Small colony of plants spreading asexually via air layering of stems and possibly also seed at edge of disturbed, upland, mixed-pine hardwood, adjacent to historic Beaton Creek Road, ca. 500 m NW of the Henderson State University Simonson Biological Field Station, Bismarck, 34.2972222, -093.2675, 11 Dec 2014, *Serviss 8160* (HEND).

KEY TO ARKANSAS SPECIES OF *FORSYTHIA*

Forsythia suspensa and *F. viridissima* are morphologically similar and easily confused with one another; however, they may be distinguished using the following key (see Fig. 3 for internode sections showing hollow versus lamellate pith).

1. Internodes internally hollow; leaves ovate to ovate-elliptic, margins serrate along most to nearly all of the leaf _______ **F. suspensa**
1. Internodes internally lamellate; leaves oblong-elliptic, obovate-elliptic, or lanceolate, margins generally only serrate on the distal one-third to one-half of the leaf, otherwise entire _______ **F. viridissima**

SECOND OCCURRENCES IN THE ARKANSAS FLORA

Rhodotypos scandens (Thunb.) Makino (Rosaceae), black jetbead. *Rhodotypos scandens* is a scandent, deciduous shrub that is native to China, Japan, and Korea (Krüssmann 1978; Li et al. 2003). It is naturalized in several eastern states, mostly in the north, but also documented in the Southeast from Alabama and South Carolina (USDA, NRCS 2014).

Rhodotypos scandens has the ability to asexually spread via air layering when its stems come in contact with moist substrate; hence, both seed production and/or vegetative reproduction may establish naturalized populations.

Vegetatively, in Arkansas, *R. scandens* closely resembles the rare native shrub, *Neviusia alabamensis* Gray (Alabama snow wreath); however, it may be distinguished from *N. alabamensis* by its opposite leaves, solitary flowers with four, large petals, and black fruits. *Neviusia alabamensis*, contrastingly, has alternate leaves, flowers that lack petals and are generally clustered in groups of 3 to 8, and fruits that are whitish-tan to brown in color.

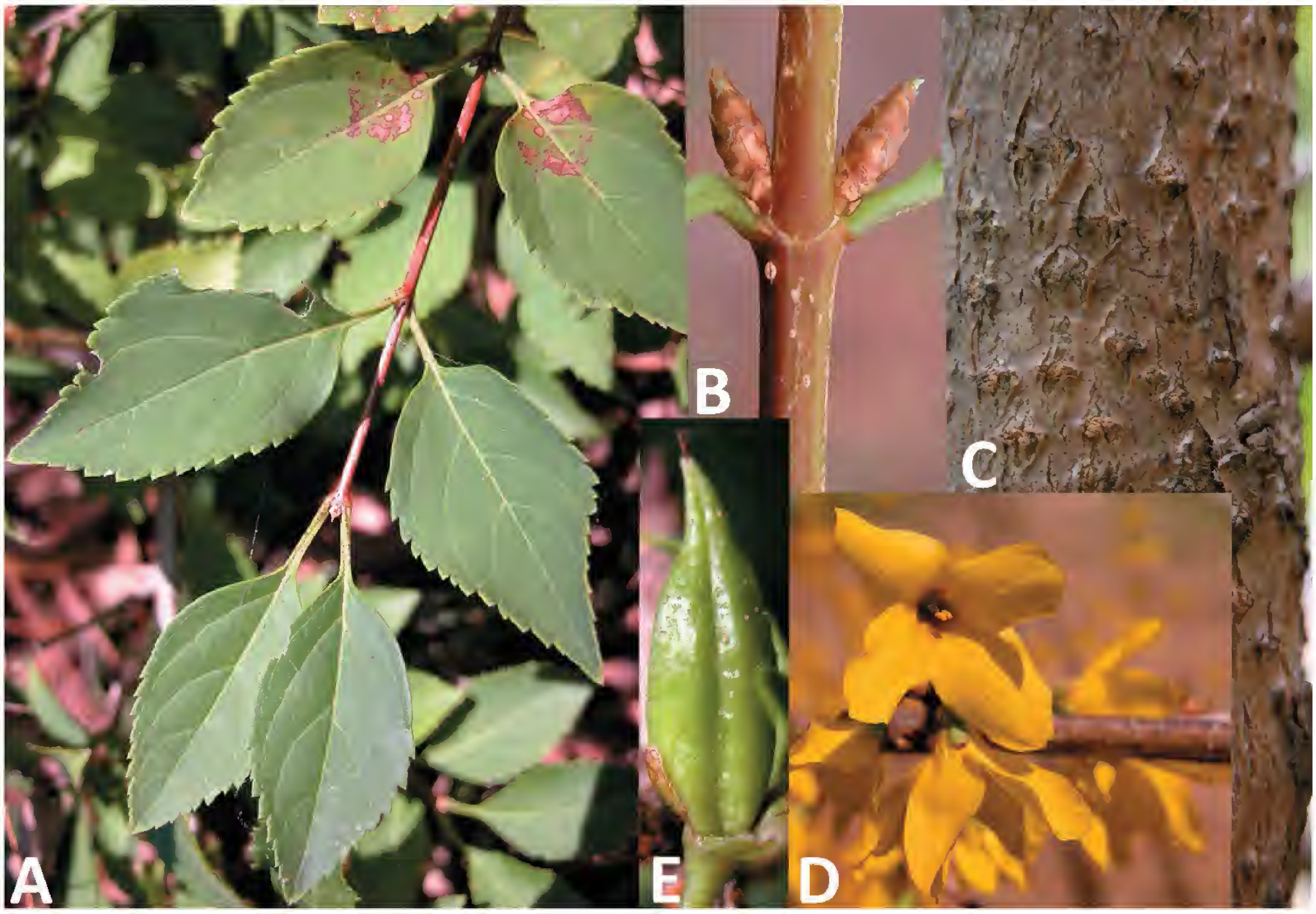

Fig. 1. Photographs of *Forsythia suspensa* (from cultivated plants). **A.** Leaves. **B.** Stem and buds. **C.** Bark. **D.** Flowers. **E.** Young fruit.

Rhodotypos scandens has only previously been documented in Arkansas from Washington County.

Voucher specimen: **ARKANSAS. Garland Co.:** several large and small shrubs along edge of small stream in open, semi-disturbed woods along riparian zone, reproductive with mature fruits, Strauss Road, ca. 1.3 mi S of highway Arkansas 88, Spring Hill Camp area, 30 Oct 2014, *Serviss 8215* (HEND).

Trachelospermum jasminoides (Lindl.) Lem. (Apocynaceae), star jasmine. *Trachelospermum jasminoides* is an aggressive, twining, evergreen liana to 10 m that is native to China (Bailey & Bailey 1976; Li et al. 1995). It has been previously documented outside of cultivation in a few southeastern states, including Florida, Louisiana, and Texas (USDA, NRCS 2014).

Trachelospermum jasminoides is commonly cultivated for its ability to rapidly form a thick, evergreen groundcover, tolerate full sun to nearly full shade conditions, and profuse production of fragrant flowers (Bailey and Bailey 1976). Stems root vigorously when exposed to bare soil or climbing substrate, such as trees or fences. It is also tolerant of dry conditions once established. The above combination of characteristics facilitates naturalization of *T. jasminoides* into novel habitats. In Arkansas, naturalized plants of *T. jasminoides* will form a dense carpet of trailing stems in the understory, but will also readily climb trees via twining and/or adventitious roots. When climbing, leaf morphology changes from the smaller, thinner leaves found on trailing stems to the larger, thicker leaves characteristically produced on climbing stems.

Trachelospermum jasminoides will readily produce fruits in Arkansas and spontaneous seedlings are sometimes encountered in the vicinity of reproductive-age plants. The seeds of *T. jasminoides* are distinctive: cinnamon-brown in color with a conspicuous coma (tuft of hairs) attached to the seed body. All parts of the plant are poisonous.

Trachelospermum jasminoides may potentially be confused with the morphologically similar, native liana,

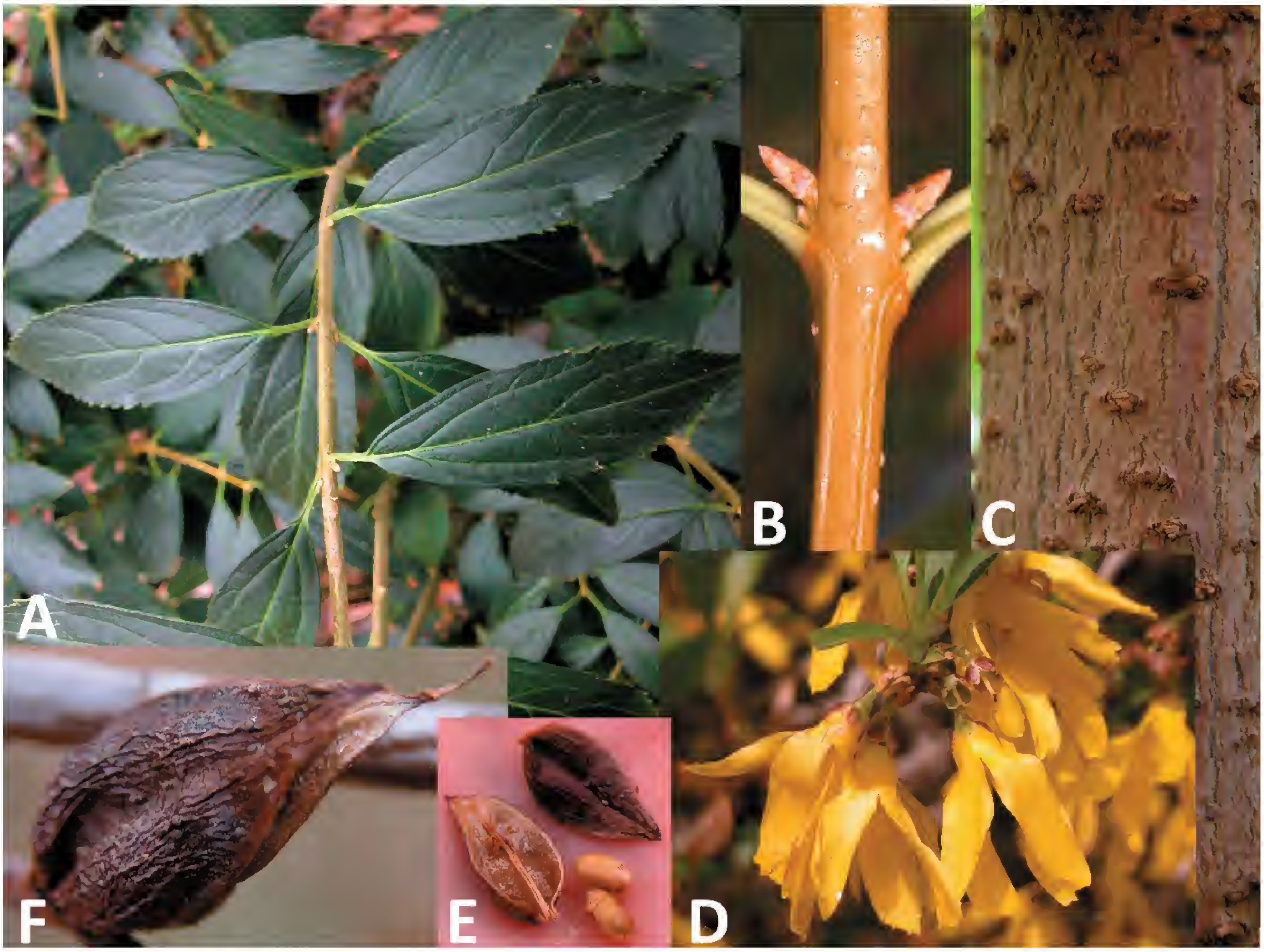

Fig. 2. Photographs of *Forsythia viridissima* (from cultivated plants). A. Leaves. B. Stem and buds. C. Bark. D. Flowers. E. Seeds and dehisced capsule. F. Mature fruit.

Gelsemium sempervirens Ait. (yellow jasmine, Carolina jasmine); however, it may be distinguished from *G. sempervirens* by its white to pale yellow flowers, elongate follicles, pubescent (when young) leaves and stems, and white, milky latex that is exuded when any vegetative portion of the plant is cut or damaged. In contrast, *G. sempervirens* has bright lemon-yellow flowers, short, elliptical capsules, foliage that is completely glabrous, and lacks milky latex.

Trachelospermum jasminoides has only previously been documented in Arkansas from Drew County.

Voucher specimen: **ARKANSAS. Clark Co.:** large expanse of plants covering ground and climbing trees, edge of stream and adjacent slope in disturbed woods of riparian zone, plants also spreading to edge of woods, plants sterile without reproductive structures, Mill Creek adjacent to the intersection of Cypress Road and Twin Rivers Drive, 34.1250000, -093.0875000, Arkadelphia, 4 Sep 2014, *Serviss 8176* (HEND).

ACKNOWLEDGMENTS

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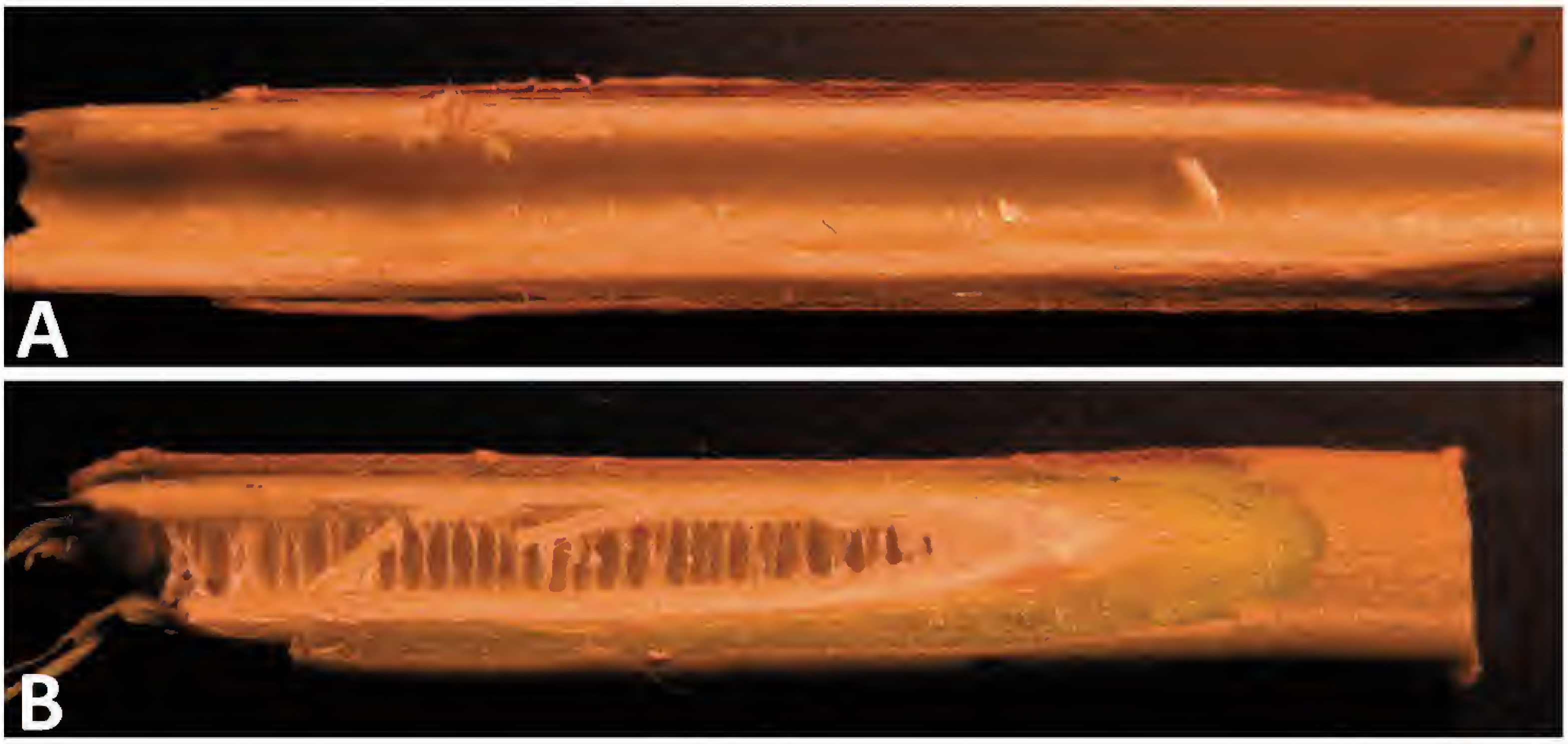

Fig. 3. Photographs of pith sections of *F. suspensa* and *F. viridissima* for comparison (from cultivated plants). A. Hollow pith of *F. suspensa*. B. Lamellate pith of *F. viridissima*.

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JOURNAL NOTICE

Douglas J. Futuyma, H. Bradley Shaffer, & Daniel Simberloff, eds. 2014 (Nov). **Annual Review of Ecology, Evolution, and Systematics, Volume 45.** (ISSN: 1543-592X; ISBN: 978-0-8243-1445-3, hbk). Annual Reviews, Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303, U.S.A. (**Orders:** www.AnnualReviews.org, science@annualreviews.org, 1-800-523-8635, 1-650-493-4400). $96.00 indiv., 665 pp., 7 ⅝" × 9 ⅜".

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NEPHROLEPIS CORDIFOLIA (NEPHROLEPIDACEAE) NATURALIZED IN SOUTHERN CALIFORNIA (U.S.A.): WITH NOTES ON UNINTENDED CONSEQUENCES OF ESCAPED GARDEN PLANTS

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ABSTRACT

Nephrolepis cordifolia occurs in many tropical, subtropical, mild-temperate, and Mediterranean regions of the world. Because it is widely cultivated, and there are many cultivars, populations have escaped from gardens and naturalized; these escapes have likely obscured its ancestral native distribution. *Nephrolepis cordifolia* is also frequently cultivated in southern California, especially for groundcover since it adapts well to a variety of soil types, tolerates full sun, and is drought-tolerant. We report here that *Nephrolepis cordifolia* grows outside of cultivation on concrete walls, trunks of palm trees, calcareous cliffs, and an ocean bluff in Los Angeles and Orange counties, coastal southern California. A naturalized population documented previously in 2006 from a streamside habitat in San Diego County was not relocated in 2014. Documentation of ornamental plants that have escaped cultivation, especially in urban habitats, is an important but often overlooked component of establishing time lag phases and early pathways of dispersal for potentially invasive plant species introduced to new regions. We provide notes on identification of *N. cordifolia*, its native and introduced ranges, garden plants and invasive weed introductions, and discussion of naturalized habitats in southern California. We also cite voucher specimens and photographic documentation of the occurrence of this species in southern California.

RESUMEN

Nephrolepis cordifolia ocurre en muchas regiones tropicales, subtropicales, semitempladas y mediterráneas del mundo. Debido a que está ampliamente cultivada, y hay muchas variedades, las poblaciones se han escapado de jardines y naturalizado; estos escapes probablemente han oscurecido su distribución nativa ancestral. *Nephrolepis cordifolia* también se cultiva con frecuencia en el sur de California, especialmente para cubierta vegetal ya que se adapta bien a una variedad de tipos de suelo, tolera pleno sol, y es tolerante a la sequía. Presentamos aquí que *Nephrolepis cordifolia* crece fuera del cultivo en las paredes de hormigón, troncos de palmeras, acantilados calcáreos, y un acantilado al mar en los condados de Los Ángeles y Orange, en el sur de la California costera. Una población naturalizada documentada previamente en 2006 a partir de un hábitat ribereño en el condado de San Diego no fue localizada en 2014. La documentación de plantas ornamentales que se han escapado de cultivo, sobre todo en hábitats urbanos, es importante pero a menudo se pasa por alto el componente de establecimiento de fases de retraso en el tiempo y principios de las rutas de dispersión de las especies de plantas potencialmente invasoras introducidas en nuevas regiones. Proporcionamos notas sobre la identificación de *N. cordifolia*, sus rangos nativos e introducidos, las plantas de jardín y las introducciones de malezas invasoras, y la discusión de los hábitats naturalizados en el sur de California. También citamos especímenes testigo y la documentación fotográfica de la presencia de esta especie en el sur de California.

KEY WORDS: *Nephrolepis cordifolia*, California, ferns, invasive garden plants, non-native plants, ornamental horticulture

INTRODUCTION

Nephrolepis (variously placed in Lomariopsidaceae or Nephrolepidaceae), a genus of ferns found mostly in tropical and subtropical regions, comprises 19 species and three varieties based on the treatment by Hovenkamp and Miyamoto (2005). It is a distinctive and an easily recognized genus, which is identified primarily by its wiry stolons, medial to often supramedial or submarginal soral position and shape, linear one-pinnate fronds, and articulate pinnae (Mickel & Smith 2004). *Nephrolepis* is sometimes placed in its own family, Nephrolepidaceae, or in the Lomariopsidaceae (Smith et al. 2006), but historically was included in Davalliaceae or Dryopteridaceae (e.g., Mickel & Smith 2004; Hovenkamp & Miyamoto 2005).

Species of *Nephrolepis* have been cultivated since the early 20th century and many remain popular today (Hoshizaki & Moran 2001). Tough and easy to grow, they are the most widely cultivated of all ferns (Brenzel 2007). The most notable is the "Boston fern," which originated in the late 1800s or early 1900s from a mutant

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of *N. exaltata* (L.) Schott and thereafter propagated widely for its attractive, arching fronds (Benedict 1916; Bailey 1924; Coile 1996). Today, it is frequently grown in homes and gardens and is a commercially important plant (Diggs & Lipscomb 2014). Nearly 80 named varieties and cultivars of *N. exaltata* are available from the horticultural industry (Brenzel 2007; BGCI 2014a).

Nephrolepis cordifolia (L.) C. Presl (southern sword fern, tuberous sword fern, fishbone fern, herringbone fern, ladder fern, or narrow sword fern) is also widely cultivated, and is grown frequently in pots, hanging baskets, and as a ground cover (Coile 1996; Brenzel 2007). Over 25 cultivars are known and many are grown in arid regions (Brenzel 2007; BGCI 2014b). In southern California, *N. cordifolia* is often grown for groundcover since it adapts well to a variety of soil types, tolerates full sun, is drought tolerant, and spreads rapidly in moist garden conditions (Rushing 2006; SDFS 2014).

Nephrolepis cordifolia is terrestrial, epiphytic, or epilithic (on rock) in moist to wet shady places, rain forests, coastal shrublands, wetland and riparian habitats, on epiphyte perches, particularly palm trunks, limestone ledges, cliff and rock habitats, urban areas, and around old home sites, roadsides, or waste places in Florida, Mexico, West Indies, Central America, South America, Africa, Southeast Asia, the Pacific Islands and Hawaii, Australia, and New Zealand (Nauman 1993; Bell 1998; Hovenkamp & Miyamoto 2005; NZPCN 2013; ISSG 2014). Because *N. cordifolia* is frequently cultivated, its nativity is often questionable. *Nephrolepis cordifolia* is said to be “indigenous” (i.e., native) to Hawaii (Valier 1995; Palmer 2003; SI 2014), but this is suspect because the species was not included in the comprehensive fern flora of Hawaii compiled by Hillebrand (1888; see also Hovenkamp & Miyamoto 2005), and it also grows in portions of northern Australia, but it is widely regarded as naturalized in the Sydney, Melbourne, and Perth regions (Bell 1998; Weeds of Australia 2014). *Nephrolepis cordifolia* has also naturalized on the southern Cook Islands (McCormack 2007) and on Moorea, French Polynesia (Murdock & Smith 2003). *Nephrolepis cordifolia* is apparently not native to Florida (FLEPPC 2014), New Zealand (NZPCN 2013; ISSG 2014), Africa (Crouch et al. 2011), temperate and tropical Asia (ISSG 2014; USDA, GRIN 2014), and elsewhere (Weber 2003). Hoshizaki and Moran (2001), however, gave the native range of *N. cordifolia* as tropical America, Africa, Asia, Australia, Japan, and New Zealand.

Nephrolepis cordifolia is also probably not native to Mexico or Central America because many specimens cited in the literature are from gardens, confused with closely related species, and/or plants may have naturalized at some localities (Mickel & Smith 2004). Therefore, *N. cordifolia* may be native only in the central portion of its known range in the Americas, i.e., Greater Antilles and Venezuela (Hovenkamp & Miyamoto 2005). A review of Old World specimens at UC (by A.R. Smith, December 2014) indicates the oldest collections come from Asia and the Pacific Region, including: New Caledonia, 1870; China, Hainan, 1878; India, 1891; Australia, 1900; Java, 1904; New Zealand, 1904; Philippines, 1907; and Madagascar, 1915, but not the Neotropics. Accordingly, the nativity of *N. cordifolia* throughout its known range, and the location of escaped garden plants and date of introductions, which has contributed to this confusion, is in need of critical review.

In the continental United States and its territories, *N. cordifolia* is reported for Alabama, Florida, Georgia, Hawaii, Puerto Rico, and the Virgin Islands (USDA, NRCS 2014). *Nephrolepis cordifolia* was not reported for California in The Jepson Manual, Second Edition, or online by the Jepson Flora Project (Baldwin et al. 2012; Jepson Flora Project 2014). *Nephrolepis cordifolia* also was not included in other California publications that identify non-native species growing spontaneously outside of cultivation, including Hrusa et al. (2002), Roberts et al. (2004), Rebman and Simpson (2006), Clarke et al. (2007), DiTomaso and Healy (2007), Dean et al. (2008), and Roberts (2008). The Consortium of California Herbaria (CCH 2014) posts several collections from cultivated sources; however, it also cites one naturalized population (with tubers) for San Diego County (*Cain et al. 134*, SD). This population was first documented in 2006 from a streamside habitat at Chollas Lake Community Park (CCH 2014). It was not relocated by R.E.R in 2014.

Nephrolepis cordifolia is reported here as naturalized, but uncommon, on calcareous cliffs and an ocean bluff in native plant communities, and it is epiphytic on the trunks of palm trees and grows in joints of rough-grouted masonry or concrete walls in urban areas in coastal southern California. At the cited localities, it appears to propagate, either through spores, tubers, or stolons, without the aid of human intervention and intentional summer-watering. It is to be expected elsewhere in similar habitats at other coastal localities. We provide notes on identification, native and introduced range, garden weeds and invasive plant introductions, and discussion of naturalized habitats for this species in southern California, as well as cite voucher specimens and photographic documentation.

Vouchers: **U.S.A.: CALIFORNIA: Los Angeles Co.:** City of Long Beach, N of E 2nd St. and W of Marine Stadium Park, Alamitos Bay, near docks on Bay Shore Ave. at E Broadway St., 33°45'35.6400"N, 118°07'43.3609"W, elev. ca. 4 m, local on palm tree trunk, 27 Jul 2014, *Riefner 14-258* (CAS, CDA, RSA, UC, UCR); City of Long Beach, N of E 2nd St. and W of Marine Stadium Park, Alamitos Bay, near docks on Bay Shore Ave. between Monroe Ave. and E Vista St., 33°45'37.0260"N, 118°07'30.2406"W, elev. ca. 6 m, local on palm tree trunks, 27 Jul 2014, *Riefner 14-261* (RSA, UC, UCR). **Orange Co.:** City of Laguna Beach, N side of North Coast Highway, N 0.25 mi from Jasmine St., 33°32'42.1764"N, 117°47'28.0201"W, elev. ca. 20 m, rare, crevice in cinder block wall along sidewalk, spreading from adjacent cultivated sources, 14 May 2010, *Riefner 10-35* (UC); City of Laguna Beach, Aliso Beach County Park, bluff ca. 0.15 mi SE of Aliso Way, NW ca. 0.25 mi of West St., 33°30'28.079"N, 117°45'12.265"W, elev. ca. 10 m, uncommon, seepage area on ocean bluff beyond the salt-spray zone, 25 Aug 2011, *Riefner 11-120* (RSA, UC); City of Yorba Linda, southbound 91-Freeway at 55-Freeway interchange ca. 0.6 mi W of Lakeview Ave., 33°55'33.9528"N, 117°49'33.1985"W (approximate), elev. ca. 80 m, locally common, expansion joints in north-facing rough-grouted concrete wall, 5 Apr 2013, *Riefner 13-59* (CAS, UC); City of Dana Point, W ca. 0.1 mi from Island Way along Dana Point Harbor Dr., cliff slope immediately S of Santa Clara Ave. and Amber Lantern St., 33°27'48.3192"N, 117°42'05.4726"W, elev. ca. 3–11 m, scattered clumps on cliff, in crevices and on and beneath ledges, 24 Feb 2014, *Riefner 14-64* (CDA, RSA, UC, UCR); City of Newport Beach, Cliff Drive Park, along Cliff Dr. near Beacon St., 33°37'13.4472"N, 117°55'26.8840"W, elev. ca. 44 m, large clump growing on palm tree trunk, 14 Jun 2014, *Riefner 14-171* (CAS, CDA, RSA, UC, UCR). **San Diego Co.:** City of Lemon Grove, Chollas Lake Community Park, E of Hidden Cove, 32°738N, 117°0637W, elev. ca. 139 m, south-facing slight slope near stream, tubers present, 27 Mar 2006, *Cain et al. 134* (SD; CCH 2014).

Identification

Nephrolepis cordifolia is a tuft-forming plant with erect to spreading rhizomes and stolons that produce long runners, with or without 1–3 cm wide scaly tubers. The upright evergreen fronds are once pinnate and grow 30–120 cm tall and 3–7 cm wide. Fronds often arch, producing a graceful habit pleasing to fern enthusiasts and gardeners.

With fertile mature fronds, most species of *Nephrolepis* are relatively easy to identify. The separation of closely-related taxa, however, which include *N. pectinata* (Willd.) Schott, *N. pendula* (Raddi) J. Sm., and *N. undulata* (Afzel. ex Sw.) J. Sm., can be problematic. Identification of *N. cordifolia* versus *N. exaltata* may also prove troublesome. With very limited sampling, Hennequin et al. (2010) found that four samples of *N. cordifolia* did not form a clade, with the sole sample of *N. exaltata* being sister to only one of the samples of *N. cordifolia* and one sample of *N. cordifolia* falling well outside the other three; however, two of their samples, including the most disparate one, were both cultivated specimens, obtained from GenBank (vouchers not seen by the authors). These preliminary results suggest that further sampling of both native and cultivated plants needs to be done before there is a clear understanding of species circumscriptions and relationships. Distinguishing features that serve to separate *N. cordifolia* from similar taxa include: conspicuously auricled basiscopic bases of pinnae; pinnae with blunt to rounded apices; dense scaly, pale rachis indument with bicolored scales (pale with dark point of attachment); indusia that are reniform to lunate; and the common presence of scaly tubers (sometimes absent; Coile 1996; Mickel & Smith 2004; Hovenkamp & Miyamoto 2005). Important characters are shown in Figs. 1 & 2.

Southern California Naturalized Populations

On coastal cliffs (Fig. 3) and an ocean bluff, *N. cordifolia* grows on calcareous substrates outside the salt-spray zone, but within the influence of moisture-laden ocean fogs and often seepage areas. Laboratory analysis (conducted by Wallace Labs, El Segundo, California) indicates these substrates are slightly to moderately alkaline (7.4–7.9 pH) and high in lime (calcium carbonate). Another non-native fern that favors mesic calcareous outcrops and old masonry, *Cyrtomium falcatum* (L.f.) C. Presl (holly fern), grows on outcrops with, or in close proximity to, *N. cordifolia* at the Dana Point and Laguna Beach locations.

In urban areas, *N. cordifolia* is epiphytic on the trunks of palm trees (Fig. 4), where moist ocean breezes provide a year-round source of moisture. *Ficus rubiginosa* Desf. ex Vent. (rusty fig, Port Jackson fig), native to eastern Australia and also widely cultivated, was reported recently for California by Dean et al. (2008). It co-occurs with *N. cordifolia* at several locations, including calcareous outcrops and cliff habitats, and it is also epi-

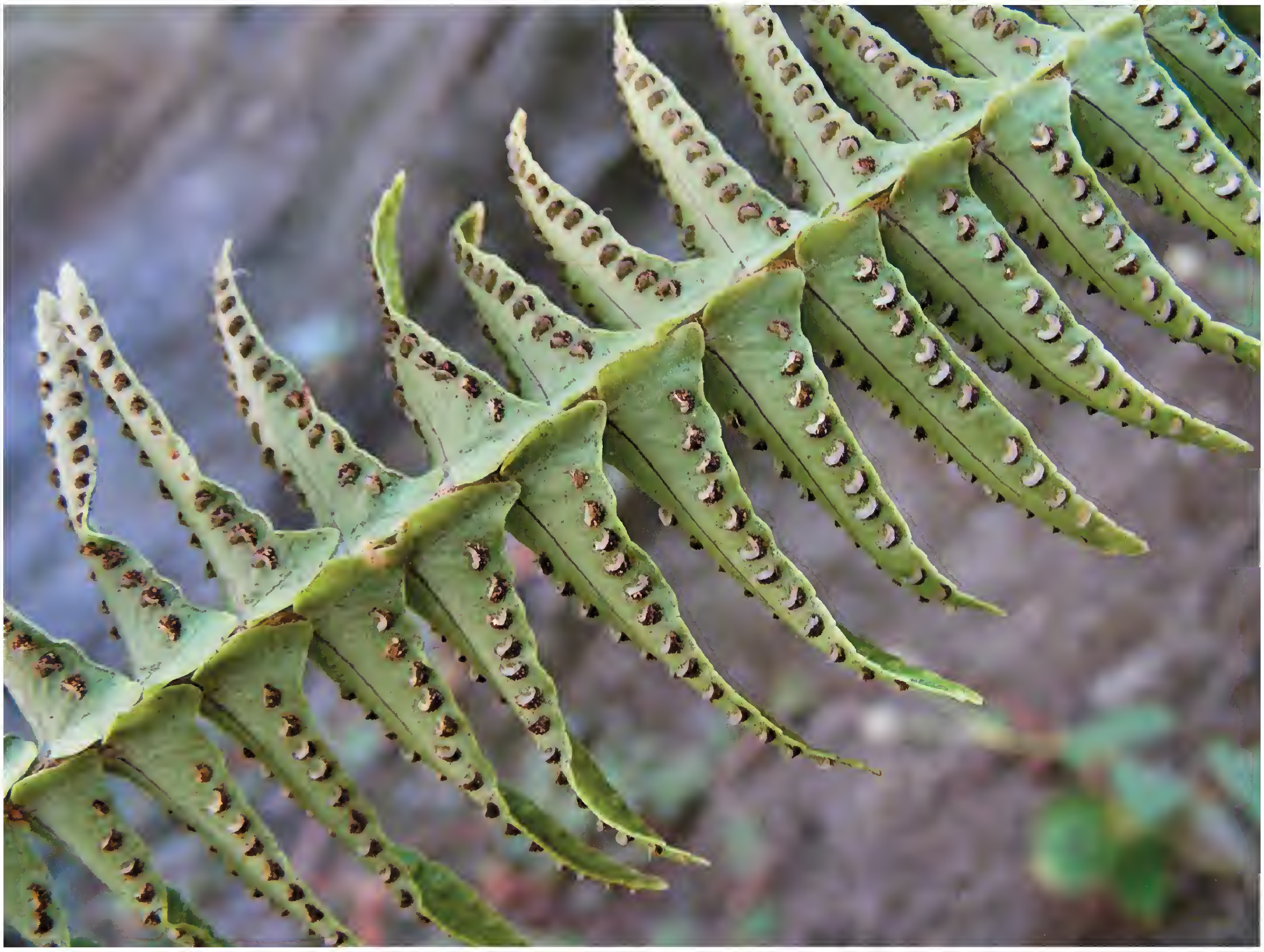

Fig. 1. Abaxial surface of a frond showing indusiate sori and auriculate overlapping base of pinnae typical of *N. cordifolia*. Photograph was taken at Dana Point population, Orange County, California.

phytic on the trunks of palm trees (Fig. 5). Metropolitan areas are particularly vulnerable to alien species introductions, which serve as entry pathways for invasions from the urban environment to native ecosystems (van Ham 2013). *Nephrolepis cordifolia* also grows in the joints of old masonry and concrete walls (Fig. 6), apparently where urban water runoff provides deep wetting within the concrete joints; this enables establishment and survival of the species in arid southern California.

The naturalized population of *N. cordifolia* documented previously in 2006 from a streamside habitat in San Diego County, although not relocated in 2014, may indicate that moist-soil or shady riparian situations could represent suitable habitat for the species elsewhere in southern California. Therefore, additional populations of *N. cordifolia* will likely be identified at new localities on calcareous outcrops and cliffs, concrete walls and masonry, trunks of palm trees, and in alkaline-soil riparian communities in coastal southern California.

The presence or absence of tubers has long been a topic of interest for this species. They appear to be functioning for water storage and not for starch (Morton 1958). With the exception of rock and concrete crevices, some plants within each of the naturalized populations of *N. cordifolia* documented herein support tubers, which can be locally abundant on underground and aerial runners. New plantlets can form from tubers and water reserves can be used during drought (Hovenkamp & Miyamoto 2005). Accordingly, tuber presence may play an important role for the establishment and persistence of *N. cordifolia* when growing outside of cultivation in summer-dry southern California.

Escaped Garden Plants and Invasive Weed Status

Escaped horticultural plants are an important source of invasive species introductions (Mack & Lonsdale

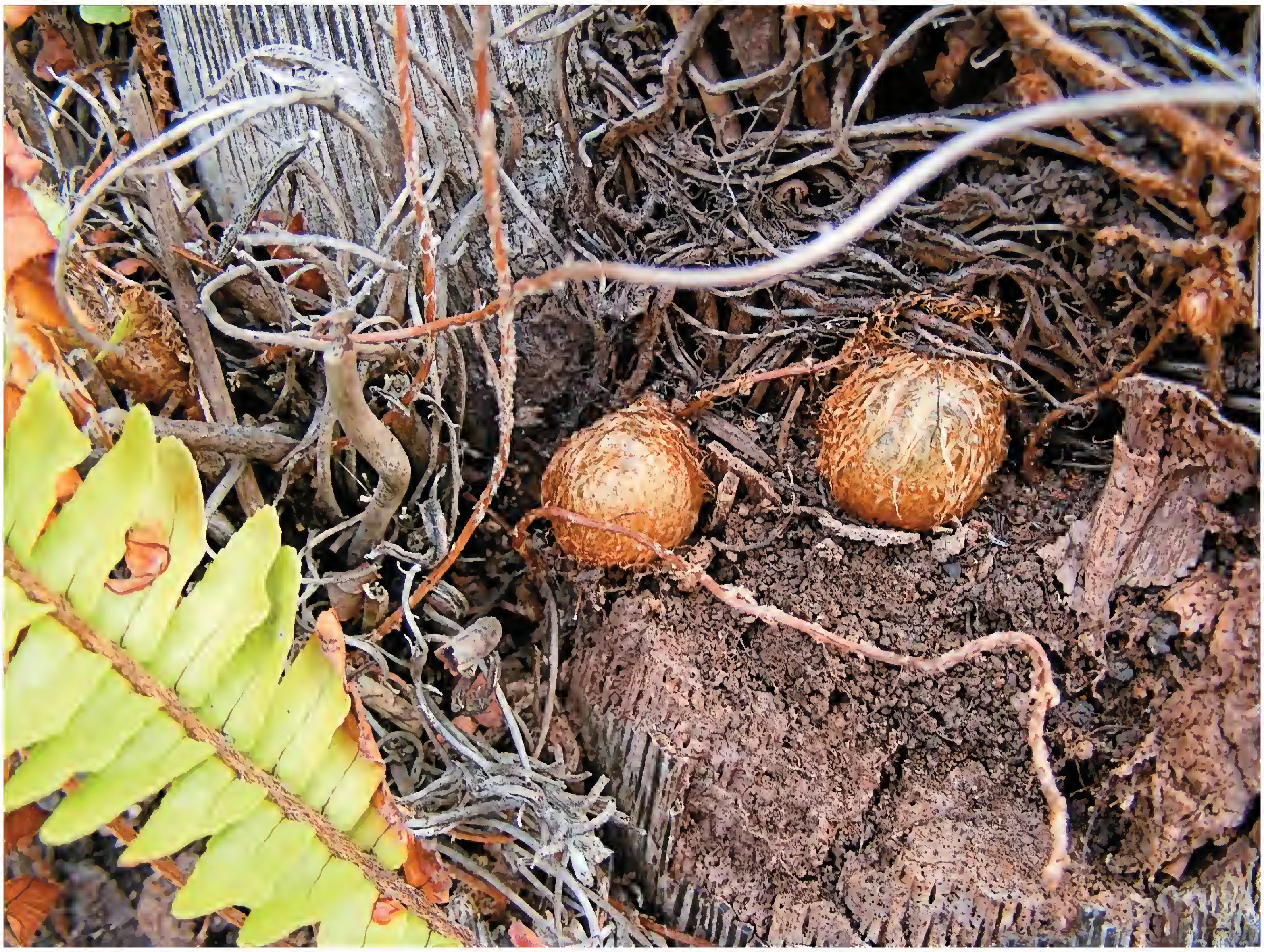

Fig. 2. ***Nephrolepis cordifolia*** **rhizomes, stolons, and scaly tubers, and adaxial frond surface with pale indument along the rachis. This photograph was taken of plants growing on the trunk of a palm tree in Long Beach, Los Angeles County, California.**

2001; Reichard & White 2001; Mack & Erneberg 2002). Of the 117 non-native plants reported for California by Dean et al. (2008), 49 of these species are available in the horticultural trade, were documented spreading from home sites, and/or are intentionally cultivated, and another eight species were first documented in California as contaminants in nurseries. Garden plant introductions are also an important source of naturalized weeds in Australia; of the 2,779 introduced plant species established in the Australian environment, approximately 1,831 (66%) represent escaped garden plants (Groves at al. 2005). In Europe, it is estimated that 80% of the currently known invasive alien plants were initially introduced as ornamental or agricultural plants (Hulme 2007). In fact, invasive garden plants comprise over half (56%) of the 36 land and aquatic plants included on the list of the *100 World's Worst Invasive Alien Species* (Lowe et al. 2000; Groves et al. 2005).

Nephrolepis cordifolia is a known threat to native plant species. In Florida, it can form dense stands and by aggressive spreading, it can displace native vegetation (Langeland et al. 2008; ISSG 2014). Accordingly, it is listed as a 'Category I' invasive plant (FLEPPC 2014). In New Zealand, it is listed as an environmental weed (Howell 2008), and is included on the 'National Pest Plant Accord' preventing the sale, cultivation, and distribution of the plant (NZPCN 2013; NPPA 2014). *Nephrolepis cordifolia* is also regarded as an environmental weed outside its native range in Australia, declared noxious in New South Wales, and prohibited from entry into Western Australia (Groves et al. 2005; SOWN 2014; Weeds of Australia 2014).

Invasive plants are always a concern when they become established in the natural ecosystems of new regions. It is widely recognized that there is often a lengthy lag phase between the time when a species becomes naturalized and represents an innocuous introduction, to when it may become highly invasive and a pest in

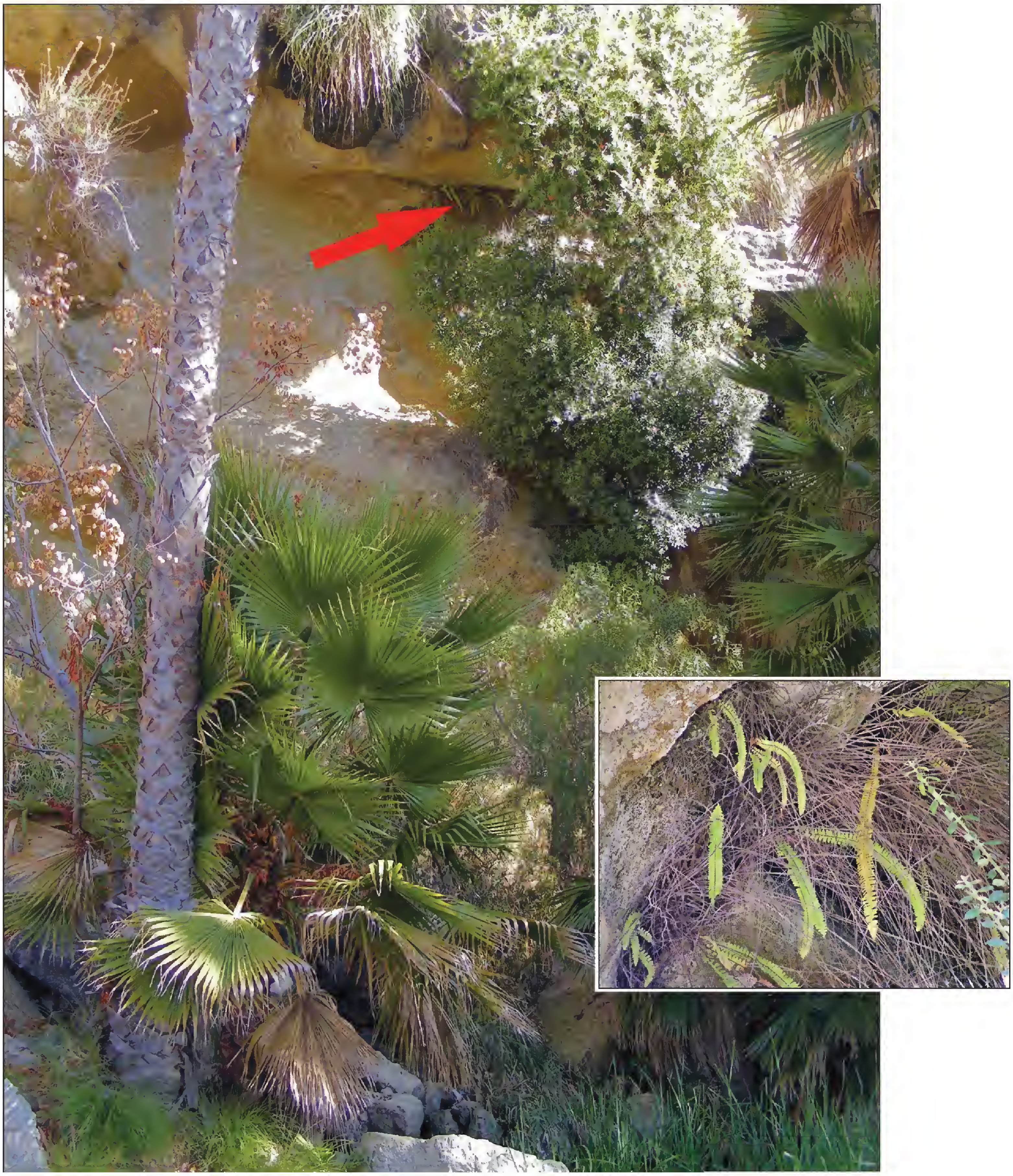

Fig. 3. The calcareous sandstone habitat of Dana Point, Orange County, California. Red arrow points to one of the clumps of *N. cordifolia* discovered on these cliffs and the inset shows a close-up of the population observed during the severe drought of 2014.

native ecosystems. These transitional stages (beginning with problematic garden weeds or urban waifs that sometimes become pest plants in native ecosystems) have usually proved to be unpredictable and unexpected (EBGC 2014).

To date, preliminary surveys indicate that *N. cordifolia* is an uncommon garden escape in southern California. However, observations by gardeners may provide insights to its potential problematic behavior. In 2005, a gardener in Acton, Los Angeles County, California, posted comments online indicating that *N. cordifo-*

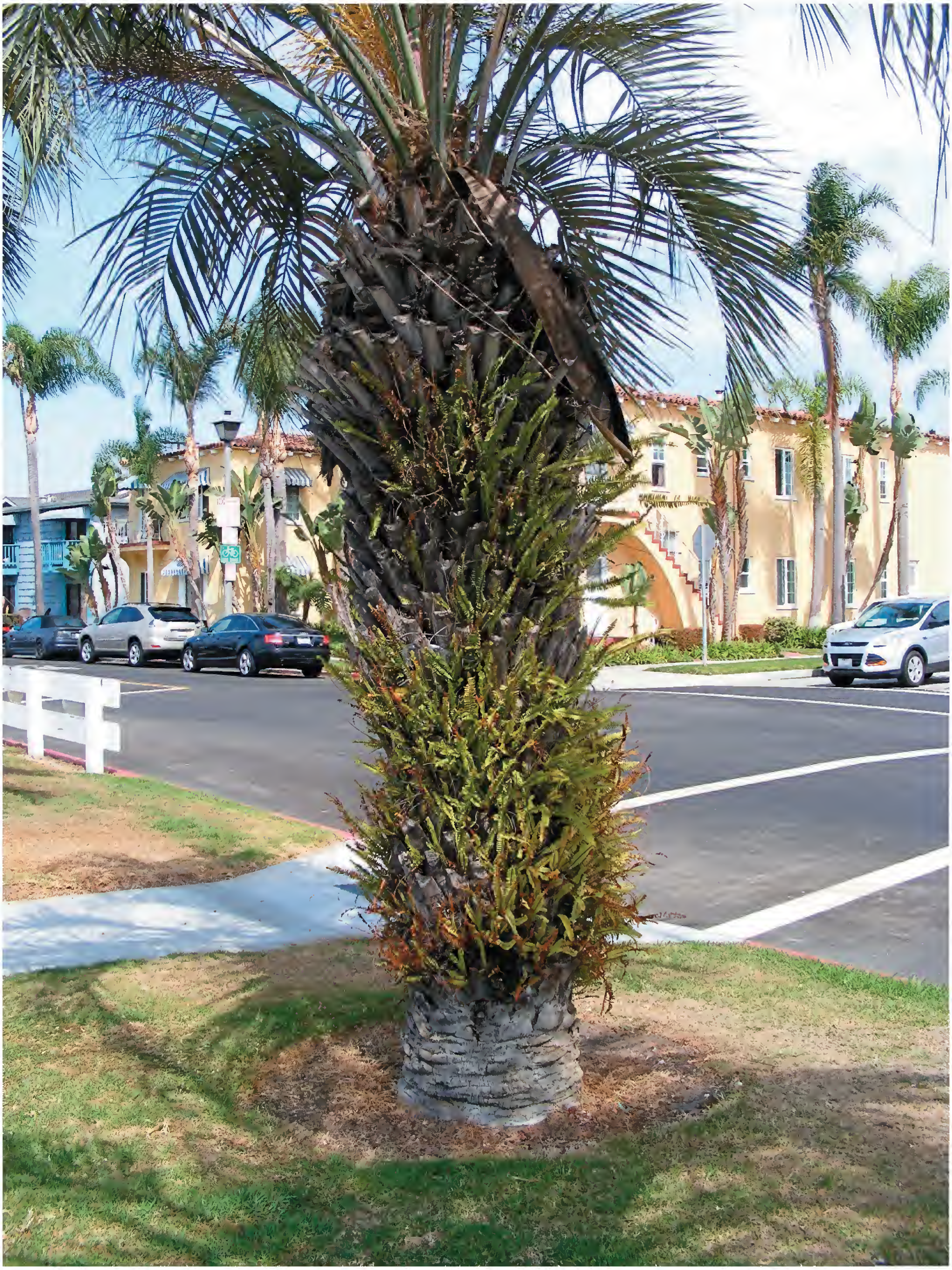

Fig 4. Photograph of *N. cordifolia* that has successfully established and is persistent on the trunk of palm trees in Long Beach, near Alamitos Bay, Los Angeles County, California.

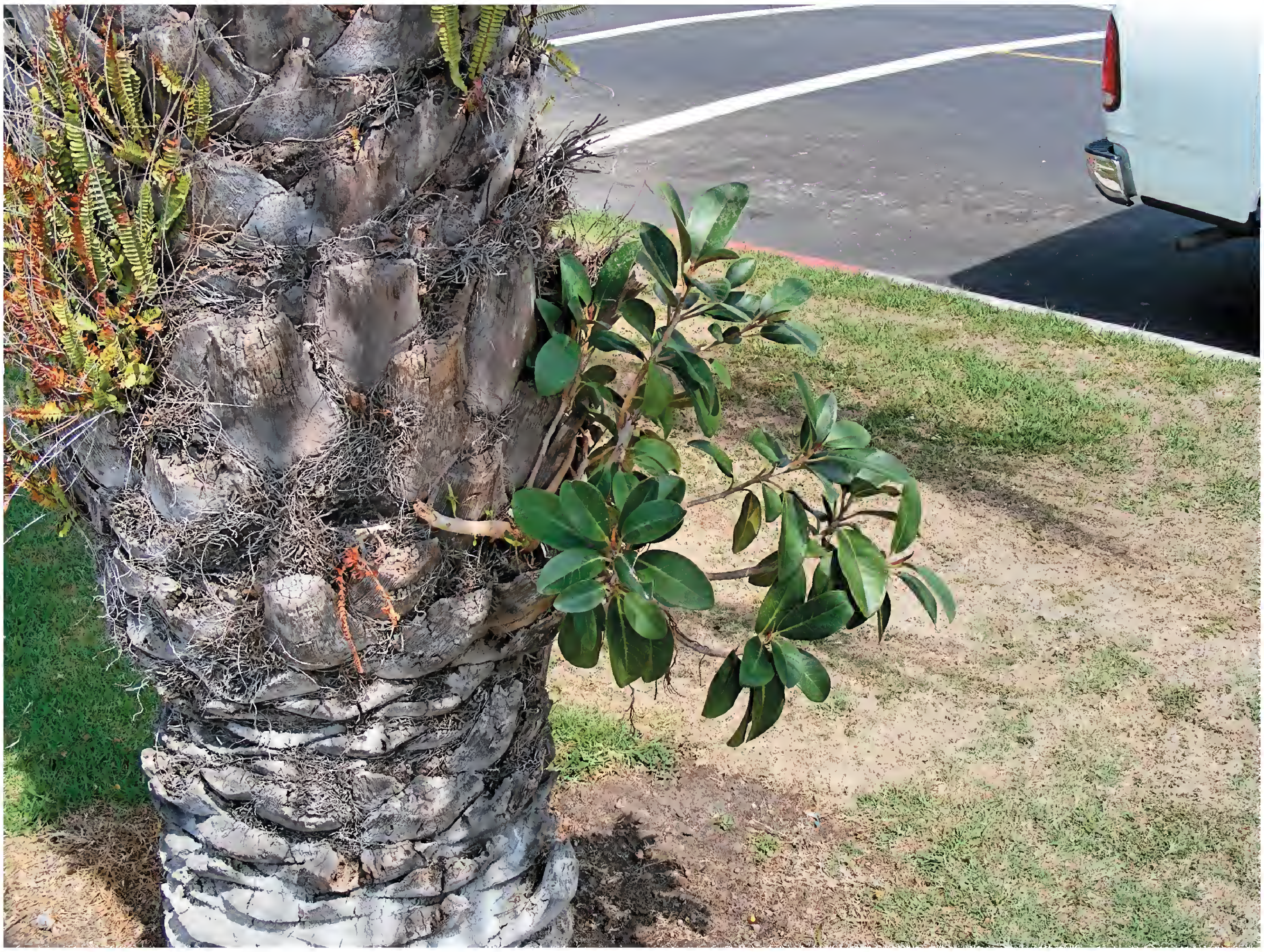

Fig. 5. ***Ficus rubiginosa*** **epiphytic on a palm tree trunk growing with** ***N. cordifolia*****. Maritime breezes off Alamitos Bay, Long Beach, California, likely provide the moisture needed for each of these species to successfully establish and persist in urban environments.**

lia is "very hardy here in hot, dry southern California … and quite invasive. … It is grown very commonly down here and sold all over as an indoor as well as an outdoor fern. … Spreads like wild fire" (Dave's Garden 2014). We do not know if *N. cordifolia* will become a pest plant in California, but it is expected to expand its range and establish elsewhere because of high propagule pressure associated with widespread cultivation. Riparian communities in watersheds affected by perennial urban runoff may be particularly vulnerable to invasions. Once established, seasonal flood scour may wash fragments of stolons or tubers downstream to colonize new habitats.

Ancestral Range, Cultivar Introductions, and Additional Research

The ancestral native range of *N. cordifolia* is obscure, in part because numerous cultivars have been developed that are widely grown in gardens and escape. These escapes have expanded the known range of the species, but have also led to ongoing confusion regarding nativity of the species in many regions (Weber 2003; Mickel & Smith 2004; Hovenkamp & Miyamoto 2005). The distribution and native versus non-native habitat occurrences documented in Australia are a good case-in-point. *Nephrolepis cordifolia* is thought to be native to parts of northern Australia, i.e., coastal eastern Queensland and parts of northeastern New South Wales, but it is regarded as naturalized in some habitats and areas outside its natural distribution in these districts (Bell 1998; Weeds of Australia 2014). It has also naturalized in Victoria, coastal southwestern Western Australia, Norfolk Island, and other areas beyond its native range such as the coastal districts of central New South Wales (Bell 1998; Weeds of Australia 2014). Although presumably the same species, the native Australian form of *N. cordifolia* is not invasive like the non-native plants thought to have been imported from Asia (SOWN 2014).

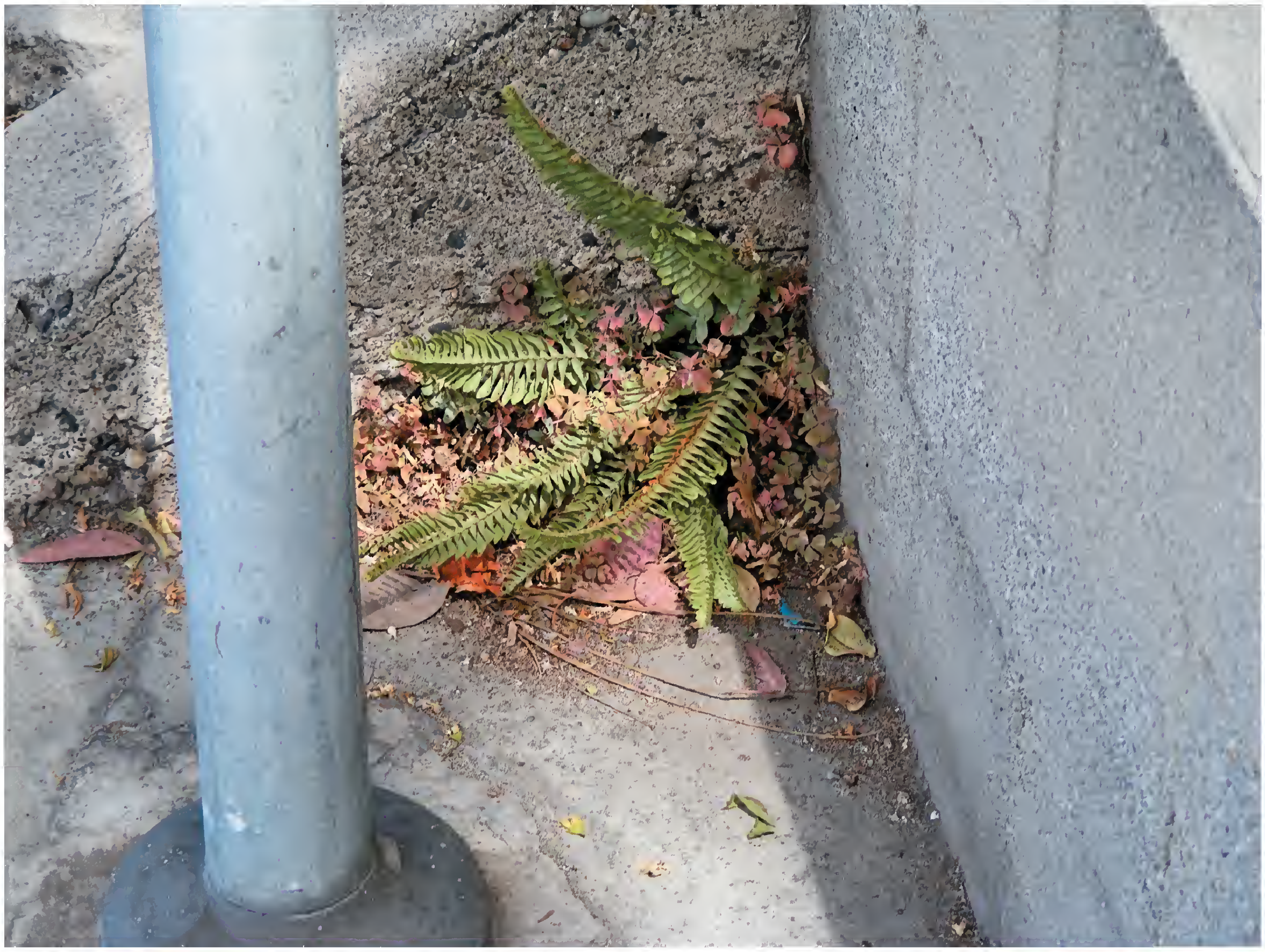

Fig. 6. ***Nephrolepis cordifolia*** **grows in the joints of old masonry and concrete walls in areas that receive urban water runoff. Photograph taken along Pacific Coast Highway in Laguna Beach, Orange County, California.**

In New Zealand, Hovenkamp and Miyamoto (2005) note the confusion between native occurrences versus introduced forms of *N. cordifolia*, but treated the native forms within the broad circumscription of *N. cordifolia* sens. str. De Lange et al. (2005), however, reinstated *N. flexuosa* Colenso, native to Fiji, Norfolk Island, Raoul Island, Lord Howe Island, and New Zealand, to help protect the indigenous populations while identifying *N. cordifolia* as the widespread naturalized and invasive plant. *Nephrolepis flexuosa* differs by its graceful stature, more narrow straight-sided fronds, is teraploid with larger spores, and lacks tubers, but may be difficult to separate from depauperate forms of *N. cordifolia*, which usually lack tubers (De Lange et al. 2005). Hovenkamp and Miyamoto (2005) coin the name *N. cordifolia* var. *pseudolauterbachii* Hovenkamp & Miyam. for seemingly very similar, tuberless plants from Fiji and Samoa. Detailed morphological, molecular, and cytological studies and intensive surveys of escaped cultivars and naturally occurring populations are needed to resolve these issues.

CONCLUSIONS

Species beginning to escape cultivation often receive little attention by botanists, largely because of the difficulty in identifying them before they are documented and published in local or regional floras. A time lag in plant invasions, which is a phase when plants are difficult to find and identify during early dispersal, is an important part of a typical invasion scenario (Schierenbeck et al. 2007). Often overlooked, documentation of garden plants escaping in urban habitats could provide important information that can be used to track the early dispersal and naturalization of these plants in new regions. In the case of *Ficus rubiginosa*, careful documentation of its early detection on brick and stone walls and on other trees in urban areas of Auckland, New Zealand, provided important information regarding its establishment and spread in the region (Gardner & Early 1996); *F. rubiginosa* is often associated with *N. cordifolia* in southern California. Early detection is an important and fundamental management objective when dealing with invasive plant species (Rejmánek 2000). Accordingly, continuing documentation of either species could provide important information regarding early detection, establishment, stepping-stone urban habitats, and frequency of occurrences in native ecosystems needed to identify time lag phases of potentially invasive species in southern California.

Ornamental horticulture has unintentionally promoted the introduction of potentially invasive species to new regions (Dehnen-Schmutz & Touza 2008). The selection and cultivation of easy-to-grow, drought hardy, salt tolerant, soil- and climate-adapted, and self-sowing cultivars may facilitate dispersal and establishment of non-native species inadvertently escaping from gardens to native ecosystems, which may start an invasion process (Mack 2000; Anderson et al. 2006). In the case of *N. cordifolia*, its introduction and naturalization in non-indigenous regions has had unintended consequences, including serious threats to native biodiversity, and this process has also compounded confusion regarding its true ancestral range and taxonomic circumscription.

Note.—After the manuscript was accepted for publication, we identified a population of *Nephrolepis cordifolia* (*Riefner 15-101*; UC) naturalized around a natural spring and in riparian woodlands at the La Cristianita Historical Baptismal Site, Camp Pendleton, San Diego County, California. Previously, it was identified as *N. exaltata* (initial collection made by K. Stockwell in 1999) on the Consortium of California Herbaria database with additional comments that it was “presumably planted and persisting” at the site. Although we do not know if this population was intentionally planted, it is clearly naturalized in 2015.

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BUDDLEJA DAVIDII (SCROPHULARIACEAE) NATURALIZED POPULATIONS IN TENNESSEE (U.S.A.) AND ITS WOODY ASSOCIATES

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ABSTRACT

Buddleja davidii Franch. (orange-eye butterfly bush), an introduced Chinese shrub in the Scrophulariaceae, is categorically naturalized at seven sites in four new Tennessee counties from field reconnaissance in 2012–2014. *Buddleja davidii* was previously documented by herbarium specimens as escaping from cultivation in Washington County (1952), Cumberland County (1975), and Hamilton County (2010). *Buddleja davidii* has limited naturalization in Anderson, Davidson, DeKalb, and Knox counties in ruderal habitats from field observations and relative abundance values. In Tennessee, orange-eye butterfly bush was confined to culturally-disturbed habitats and was not present in natural secondary forest communities. A total of 51 woody associated species (32 native, 19 non-native) were also documented among these seven populations to obtain descriptive site data. Fifteen of 19 non-native woody associates were classified as state-listed invasive taxa, which affect the colonization of *B. davidii* populations.

Key Words: *Buddleja davidii*, woody associated species, distribution, naturalized, orange-eye butterfly bush, Scrophulariaceae, invasives, Tennessee counties

RESUMEN

Buddleja davidii Franch. (arbusto mariposa de ojos naranja), un arbusto chino introducido de Scrophulariaceae, está naturalizado categóricamente en siete sitios en cuatro nuevos condados de Tennessee a partir de estudios de campo realizados en 2012–2014. *Buddleja davidii* fue previamente documentada por especímenes de herbario como escapada de cultivo en los condados de Washington (1952), Cumberland (1975) y Hamilton (2010). *Buddleja davidii* tiene una naturalización limitada en los condados de Anderson, Davidson, DeKalb y Knox en base a observaciones de campo y valores de abundancia relativa. En Tennessee, el arbusto mariposa de ojos naranja se limitaba a los hábitats perturbados por cultivo y no estaba presente en las comunidades forestales secundarias. También se documentaron un total de 51 especies asociadas leñosas (32 nativas, 19 no nativas) entre estas siete poblaciones para obtener datos descriptivos de los sitios. Quince de las 19 especies asociadas leñosas no nativas fueron clasificadas como taxones invasivos registrados en el estado, que afectan a la colonización de las poblaciones de *B. davidii*.

Palabras clave: *Buddleja davidii*, especies leñosas asociadas, distribución, naturalizado, arbusto mariposa de ojos naranja, Scrophulariaceae, invasivos, condados de Tennessee

INTRODUCTION

Buddleja davidii Franch. (orange-eye butterfly bush, butterfly bush, or summer lilac) are unarmed, multiple-stemmed, deciduous to semi-deciduous, shade-intolerant, pioneer shrubs placed in the Scrophulariaceae of the Lamiales (Norman 2012). Orange-eye butterfly bush is native to 13 mountainous provinces in southwest and central China (Zheng et al. 2006; Tallent-Halsell & Watt 2009). *Buddleja* is comprised of 90–100 species worldwide (Stuart 2006; Dirr 2009). *Buddleja davidii* has been the most extensively planted ornamental of the ca. 25 cultivated species. At least 150 cultivars and hybrids of *B. davidii* have been recognized (Stuart 2006; Dirr 2009). *Buddleja davidii* has been selected for ornamental horticulture due to its growth hardiness in many anthropogenic habitats, attractive dark green and grayish-white foliage, fragrant white, lilac-lavender, lilac-rose, red-violet to purple flowers, and high nectar content for the attraction of butterfly, moth, bee, and wasp pollinators (Stuart 2006; Dirr 2009; Tallent-Halsell & Watt 2009).

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Buddleja davidii (herein, *B. davidii*, butterfly bush, or orange-eye butterfly bush), has a broad ecological amplitude for propagation, establishment, colonization, and naturalization in a diversity of open, insolated and weedy disturbed habitats through means of wind-dispersed seeds (Tallent-Halsell & Watt 2009; Trueblood 2009; Thompson & Abbott 2013). Butterfly bush is a fast growing, semi-cold-tolerant shrub that readily establishes populations in full sun in a wide range of nutrient poor soil types (Tallent-Halsell & Watt 2009; Trueblood 2009). *Buddleja davidii* thrives best in well-drained alkaline soils but regardless of adaptations, it is rather a short-lived shrub mostly of less than 30 years (Smales 1990; Brunel 2006; Tallent-Halsell & Watt 2009; Trueblood 2009). The presence of endophytic arbuscular mycorhizzae in *B. davidii* enhances its establishment and survival (Camargo-Ricalde et al. 2003; Dickie et al. 2007).

In Kentucky, *Buddleja davidii* was reported naturalized in five counties from active and abandoned railroad right of ways, weedy disturbed urban areas, roadside ditch thickets, lake floodplains, and severely-burned national forest lands (Thompson & Abbott 2013). In 2014, butterfly bush was documented as naturalized for a sixth Kentucky county distribution along a grassy road shoulder and guard rail in Leslie County within the Cumberland Plateau [*R.L.Thompson & K. Rivers Thompson 14-377* (BEREA, EKY)].

Our definitions of non-native "naturalized" species and "invasive" species are modified from Nesom (2000) and Richardson et al. (2000) by subjective degree of colonization, establishment, and migration. A "naturalized" plant is a non-native plant that grows naturally in ruderal or culturally-derived habitats, and is able to maintain itself for at least 10 years without anthropogenic assistance. An "invasive" plant is an aggressive, non-native naturalized plant that tends to readily spread and displace the native flora and vegetation over time. Thompson & Abbott (2013) described orange-eye butterfly bush as naturalized in Kentucky from field reconnaissance, herbarium searches, and pertinent literature. Furthermore, Thompson and Abbott (2013) determined that *B. davidii* should not be classified as an invasive species in Kentucky. Butterfly bush in six Kentucky counties was closely restricted to those ruderal habitats where it was found with little evidence of additional propagation, spread, or migration into contiguous natural vegetation.

Our major objectives were to conduct field reconnaissance searches for Tennessee populations of *Buddleja davidii*, pursue an in-depth herbarium specimen examination, review relevant literature, and compile descriptive data of the woody associated species at naturalized population sites.

BUTTERFLY BUSH NON-NATIVE STATUS

Regarding non-native origin status, *Buddleja davidii* has been classified as naturalized in Australia, Canada, Central America, Europe, New Zealand, Puerto Rico, South America, and the United States (Tallent-Halsell & Watt 2009; Norman 2012). It has been recorded as an invasive shrub in Australia, England, France, New Zealand, and in the USA states of Hawaii, Oregon, and Washington (Tallent-Halsell & Watt 2009; Young-Mathews 2011; Norman 2012; USDA, ARS 2014). In Oregon, *B. davidii* is designated as a Class "B" noxious weed; and, it is listed as a Class "C" noxious weed along riparian floodplains in Washington (Young-Mathews 2011; USDA, NRCS 2014). *Buddleja davidii* grows without cultivation in a variety of temperate habitats that include limestone quarries, coal surface-mined lands, active and abandoned railways, fallow fields, successional woodland ecotones, roadside thickets and ditch margins, riparian corridors, streambeds, floodplains, and lake shores, among numerous other disturbed habitats (Tallent-Halsell & Watt 2009; Norman 2012).

Orange-eye butterfly bush has been reported from 21 states (Kartesz 2014; USDA, NRCS 2014) to 24 states in the United States (EDDMapS 2014). Distribution maps for these states do not clarify whether the non-native status of *B. davidii* is cultivated, introduced, persisting, a waif, naturalized, or invasive among the non-native classifications of Nesom (2000). Map distributions likely represent a grouping of all those non-native categories from herbarium vouchers and literature reports.

Recent literature contains several discrepancies and inconsistencies on the invasiveness of butterfly bush within the eastern United States. *Buddleja davidii* was not listed as an invasive species in AL, FL, GA, KY, MS, NC, SC, nor TN by the SE-EPPC (2014). In contrast, the MA-EPPC (2008) reported butterfly bush as an invasive in CA, KY, NC, NJ, OR, PA, WA, and WV. Swearingen et al. (2010) listed it as a "Plant to Watch" in DE, MD, NJ, PA, VA, and WV. The KY-EPPC (2013) listed *B. davidii* for the first time, as a "Moderate Threat," an exotic plant that can spread into disturbed corridors although not readily invading natural areas. Butterfly bush has been updated to an "Alert" rank for Tennessee, an exotic plant that possesses invasive characteristics in habitats similar to those found in Tennessee (TN-EPPC 2009). Jones and Wofford (2013) indicated *B. davidii* to be a non-native escaped species of disturbed sites in Kentucky and Tennessee; and, it was expected to become more problematic in the future. Chester et al. (2015) noted that *B. davidii* is "a landscaping species, rarely naturalized in ruderal areas statewide...shows strong invasive potential."

Nevertheless, Trueblood (2009) developed an Invasive Species Assessment System data form and score sheet for *Buddleja davidii* in North Carolina. She determined *B. davidii* to have limited ecological impact, distribution, and invasive potential in natural areas. In her assessment summary, orange-eye butterfly bush was considered to be a non-invasive, shade-intolerant, short-lived pioneer shrub that tended to be controlled or eliminated mainly through processes of natural plant succession by native woody vegetation. In brief, *Buddleja davidii* has not been shown to have negative ecological impact in North Carolina natural areas.

METHODS

Field reconnaissance was conducted from 2012–2014 toward discovering naturalized populations of *Buddleja davidii* in Tennessee. Descriptive data were also recorded for woody associated species for seven populations in Knox, Anderson, DeKalb, and Davidson counties. "Associated woody species" are those characteristic or indicator taxa often found with certain other non-native and/or native species that have similar phenological life cycles, plant durations, ecological adaptations, and habitat requirements.

Relative abundance values (frequency of occurrence) for orange-eye butterfly bush and interspersed woody associates were based on the scale of Thompson (2007): Rare (R) = 1–4 individuals; Scarce (S) = 5–10 individuals; Infrequent (I) = 11–30 individuals; Occasional (O) = 31–100 individuals; Frequent (F) = 101–1000 individuals; and Abundant (A) = 1000s of individuals.

Relative frequency percentages were determined from absolute frequency by the presence of a native or non-native woody associate within each *Buddleja davidii* population site (Table 1). Relative frequency is a qualitative measure of the abundance and distribution of each associated species' occurrence within the seven *B. davidii* population sites.

Nomenclature, classification, and identification for associated woody taxa follow Jones and Wofford (2013). Herbarium acronyms for voucher specimens follow Index Herbariorum of Thiers (2014). Herbarium searches were made of the regional Tennessee university herbaria (APSC, ETSU, HTTU, MTSU, TENN, and UCHT) and other state and national herbaria (BRIT, EKY, KY, MO, NCU, and VDB).

RESULTS AND DISCUSSION

Tennessee Butterfly Bush Herbarium Collections

From herbarium specimen label data, *Buddleja davidii* was first documented growing without cultivation in Washington County on July 28, 1952 [*R.L. James 16885* (TENN)]; and, it was also documented as an escape at another site in Washington County in 1999 [*Mark Dugger 27* (ETSU)]. In 1975, *B. davidii* was reported as escaped at two locations in Cumberland County [*B. Eugene Wofford 51846* (NCU, TENN); *R. Kral 56489* (MO, VDB)]. The Washington and Cumberland counties "escaped" populations are likely the basis of *B. davidii* being classified as "naturalized" in *A Fifth Checklist of Tennessee Vascular Flora* by Chester et al. (2009). In Hamilton County, a 2010 specimen was also labeled as "commonly escapes from cultivation" [*Gary H. Morton 9203* (UCHT)]. Orange-eye butterfly bush distribution was initially mapped for Tennessee in Cumberland, Knox, and Washington counties (Chester et al. 1997; USDA, NRCS 2014), while Cumberland, Grainger, Knox, Shelby, and Washington counties were mapped by TENN (2014) and EDDMapS (2014). *Buddleja davidii* has been documented as a planted ornamental from herbarium specimens and field work in seven Tennessee counties as listed: Blount (BEREA), Bradley (UCHT), Grainger (TENN), Knox (BEREA, TENN), Putnam (BEREA), Sevier (TENN), and Shelby (TENN). Thirteen Tennessee counties have been documented by naturalized or planted butterfly bush specimens (Fig. 1).

Table 1. Woody associates for seven _Buddleja davidii_ populations in four Tennessee counties.

County Species	Knox Site 1	Knox Site 2	Knox Site 3	Ander. Site 4	Ander. Site 5	DeK. Site 6	Dav. Site 7	No. Sites	Frequency %
Acer negundo	+	+	+	+	+	+	+	7	100
**Ailanthus altissima	+	+	+	+	+	+	+	7	100
**Ligustrum sinense	+	+	+	+	+	+	+	7	100
**Lonicera japonica	+	+	+	+	+	+	+	7	100
**Lonicera maackii	+	+	+	+	+	+	+	7	100
Parthenocissus quinquefolia	+	+	+	+	+	+	+	7	100
Platanus occidentalis	+	+	+	+	+	+	+	7	100
**Albizia julibrissin	+	+	+	+	+	+		6	85.71
**Pyrus calleryana	+	+	+	+	+	+		6	85.71
**Rosa multiflora	+	+	+	+	+	+		6	85.71
Rubus occidentalis	+	+		+	+	+	+	6	85.71
Toxicodendron radicans	+	+	+		+	+	+	6	85.71
**Celastrus orbiculatus	+	+	+	+			+	5	71.43
Cercis canadensis	+	+		+	+	+		5	71.43
Juniperus virginiana	+	+		+	+	+		5	71.43
Liriodendron tulipifera	+	+		+	+	+		5	71.43
**Paulownia tomentosa	+	+	+	+	+			5	71.43
Robinia pseudoacacia	+	+	+		+	+		5	71.43
Ulmus rubra	+	+			+	+	+	5	71.43
Vitis vulpina		+	+		+	+	+	5	71.43
Celtis occidentalis	+	+	+				+	4	57.14
**Elaeagnus umbellata	+	+		+	+			4	57.14
**Euonymus fortunei		+	+		+		+	4	57.14
Fraxinus americana		+	+	+		+		4	57.14
Salix nigra			+		+	+	+	4	57.14
Acer saccharum		+	+	+				3	42.86
Ampelopsis cordata					+	+	+	3	42.86
Campsis radicans		+			+		+	3	42.86
Fraxinus pennsylvanica			+		+		+	3	42.86
Rhus glabra	+	+			+			3	42.86
Rubus pensilvanicus	+	+			+			3	42.86
Acer saccharinum			+				+	2	28.57
Carya cordiformis			+				+	2	28.57
Clematis virginiana		+			+			2	28.57
Cornus amomum			+	+				2	28.57
Frangula caroliniana	+		+					2	28.57
Gleditsia triacanthos	+				+			2	28.57
**Morus alba					+		+	2	28.57
Quercus muhlenbergii			+				+	2	28.57
*Ulmus pumila	+			+				2	28.57
Catalpa bignonioides							+	1	14.29
**Elaeagnus pungens			+					1	14.29
**Ligustrum vulgare						+		1	14.29
**Nandina domestica					+			1	14.29
*Prunus persica					+			1	14.29
**Pueraria montana		+						1	14.29
Rhus copallinum					+			1	14.29
Sambucus canadensis	+							1	14.29
Smilax rotundifolia							+	1	14.29
Ulmus americana			+					1	14.29
*Yucca filamentosa					+			1	14.29
Totals: 51 taxa	27	30	28	21	34	22	24		

Ander. = Anderson County; **DeK.** = DeKalb County; **Dav.** = Davidson County.
(*) = a naturalized taxon, (**) = an invasive pest plant for Tennessee (TN-EPPC 2009).

The four new counties with naturalized butterfly bush are discussed separately. Tennessee specimen label data on naturalized or planted shrubs from Tennessee counties are as follows:

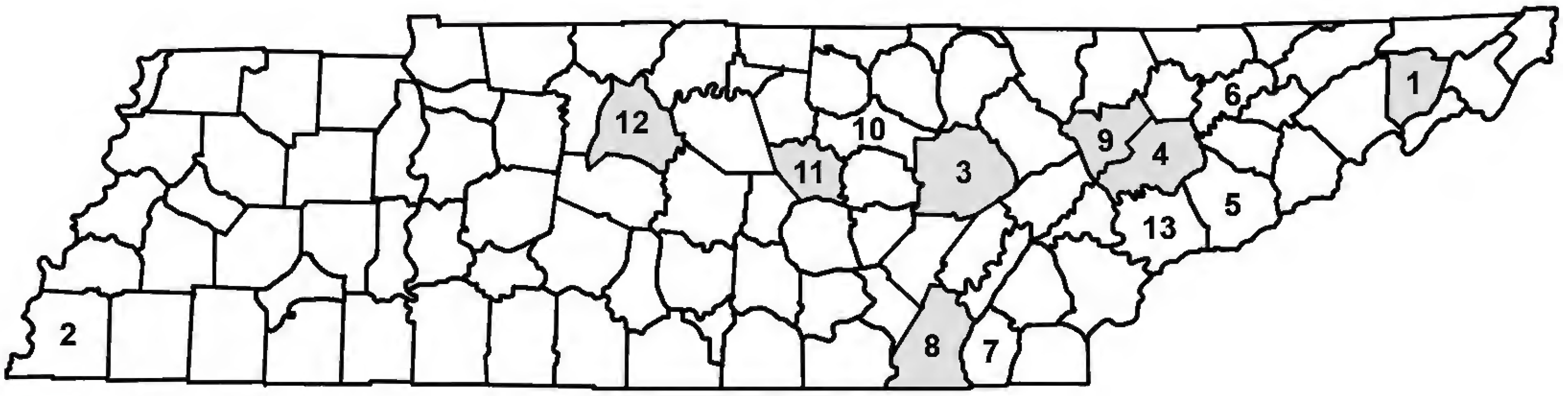

Fig. 1. Tennessee counties documented with *Buddleja davidii* specimens by collection year(s). Gray-numbered counties indicate naturalized populations; white-numbered counties represent cultivated ornamental individuals or populations: 1 = Washington (1952, 1999), 2 = Shelby (1972), 3 = Cumberland (1975), 4 = Knox (1991, 2012, 2013, 2014), 5 = Sevier (1998), 6 = Grainger (1999), 7 = Bradley (2002), 8 = Hamilton (2010), 9 = Anderson (2014), 10 = Putnam (2014), 11 = DeKalb (2014), 12 = Davidson (2014), 13 = Blount (2014). (Tennessee map adapted by Melanie G. Bentley, Eastern Kentucky University)

TENNESSEE. Blount Co.: Maryville, Maryville College, E side of Bartlet Hall Student Center lawn off Circle Drive and Morningside Lane, cultivated shrub with lilac-lavender flowers; 35.75053°N, 83.96429°W, 448 m, 29 July 2014, *R.L. Thompson & K. Rivers Thompson 14-341* (BEREA, TENN); Townsend, Great Smoky Mountain Heritage Center, 123 Cromwell Drive, off TN 73, one surviving shrub with purple flowers planted by flagpoles in front, one dead from April freeze, 35.67472°N, 83.722292°W, 344 m, 29 July 2014, *R.L. Thompson & K. Rivers Thompson 14-342* (BEREA, TENN). **Bradley Co.:** Cleveland, growing at the S side of gymnasium at Cleveland State Community College, adjacent to parking lot approximately 9 m from Adkisson Drive; shrub about 1.5 m tall, mint green color, few dark purple flowers, 220 m, 17 Mar 2002, *Anna Lea Griffith 15* (UCHT). **Cumberland Co.:** Crab Orchard, roadside along Highway 70, just W of I-40 E, Exit 329, 30 Jul 1975, *B. Eugene Wofford 51846 with W. Michael Dennis* (TENN); escape by roadside rip-rap near creek, 28 Aug 1975, *R. Kral 56489* (MO, VDB). **Grainger Co.:** Rutledge, planted on Tampico Road, 6 Sep 1999, *H.R. DeSelm s.n.* (TENN). **Hamilton Co.:** Apison, along fence row at 4312 Bill Jones Road, commonly escapes from cultivation, 9 Jul 2010, *Gary H. Morton 9203* (UCHT). **Knox Co.:** Knoxville, planted at Woodland Drive, Sequoyah Hills, 20 Oct 1991, *H.R. DeSelm s.n.* (TENN); Knoxville, Ijams Nature Center, 2915 Island Home Avenue at NW corner of William O. Miller Education Building (the Home Site), a single shrub planted in 1983, not spreading, 35.95758°N, 83.86961°W, 282 m, 29 Nov 2012, *R.L. Thompson & S. Brobst 12-1157* (BEREA, TENN); 18 May 2014, *R.L. Thompson & K. Rivers Thompson 14-120* (BEREA, TENN). **Putman Co.:** Cookeville, two shrubs planted at 2675 Lakeland Drive off I-40 E at Exit 290, US 70 (TN 24), 36.13151°N, 85.44244°W, 291 m, 15 Apr 2014, *R.L. Thompson & S.J. Stedman 14-25* (BEREA, TENN); white flowers, evident branch die-back freeze damage, 12 Jul 2014, *R.L. Thompson & G.N. Douglas 14-340* (BEREA, TENN). **Sevier Co.:** Sevierville, planted on Section Springs Road, 17 Aug 1998, *H.R. DeSelm s.n.* (TENN). **Shelby Co.:** Memphis, cultivated, Helene Griffith's home, 568 St. Nick Drive, corolla white, 21 Jul 1972, *Edward T. Browne, Jr. & Elizabeth M. Browne 72 FH.3* (TENN). **Washington Co.:** Johnson City, escaped from cultivation off Knob Creek Road near Snow Chapel Memorial Baptist Church, 28 Jul 1952, *R.L. James 16885* (TENN); Johnson City, East Tennessee State University, escaped at forest edge of the hiking trail across from Central Receiving, 20 Nov 1999, *Mark Dugger 27* (ETSU).

Reconnaissance of Tennessee Butterfly Bush Populations

Field investigations for seven naturalized *Buddleja davidii* populations and their woody associates were expedited through the assistance of six Tennessee naturalists (S. Brobst & D. Estes, pers. comm. 2012; D. Bruce, T. Crabtree, M. Smith, & S. Stedman, pers. comm. 2014). The seven population sites were discovered in Knox County (3), Anderson (2), DeKalb (1), and Davidson (1) counties; these are new county naturalized Tennessee populations. Orange-eye butterfly bush and the woody associates at each of seven sites are discussed in regards to their location, habitat, physical site characteristics, relative abundance, relative frequency, woody associated species status, and effects of *B. davidii* toward the native flora and vegetation.

Buddleja davidii naturalized in Knox County

Three naturalized populations of *Buddleja davidii* were discovered and studied in Knoxville, Knox County, Tennessee, during 2012–2014 (Fig. 2; Fig. 3). Knoxville and vicinity are situated within the Southern Limestone/Dolomite Valleys and Rolling Hills Ecoregion of the Ridge and Valley Province. Potential vegetation is a mosaic of Appalachian Oak and Mesophytic Forest often with *Juniperus virginiana* L. (Griffith et al. 1997). Forested terrain typically consists of undulating to rolling, rounded hills comprised of underlying bedrock strata from the Ordovician Holston Limestone Formation (Griffith et al. 1997).

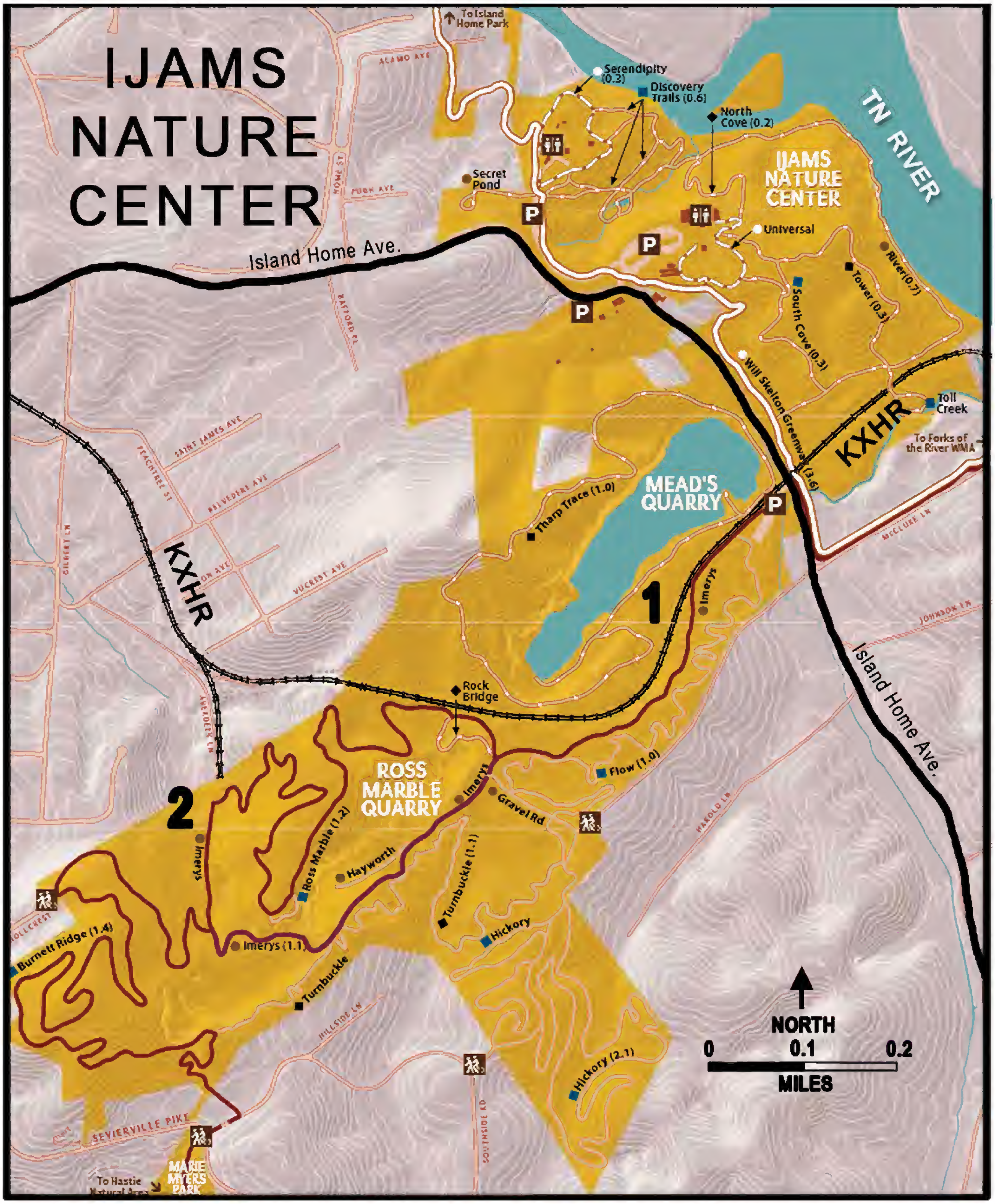
IJAMS NATURE CENTER
To Island Home Park
Serendipity (0.3)
Discovery Trails (0.6)
North Cove (0.2)
TN RIVER
IJAMS NATURE CENTER
Secret Pond
Universal
Island Home Ave.
South Cove (0.3)
Tower (0.3)
River (0.7)
Will Skelton Greenway (3.6)
Toll Creek
To Forks of the River WMA
KXHR
MEAD'S QUARRY
Tharp Trace (1.0)
1
Imerys
KXHR
Rock Bridge
ROSS MARBLE QUARRY
Flow (1.0)
Gravel Rd
Imerys
2
Imerys
Ross Marble (1.2)
Hayworth
Turnbuckle (1.1)
Hickory
Burnett Ridge (1.4)
Imerys (1.1)
Turnbuckle
Hickory (2.1)
Island Home Ave.
NORTH
0
0.1
0.2
MILES
SEVIERVILLE PIKE
To Hastie Natural Area
MARIE MYERS PARK
ALAMO AVE
PUGH AVE
HOME ST
RAFFORD PL
SAINT JAMES AVE
BELVEDERE AVE
PEACHTREE ST
VUCREST AVE
GILBERT LN
ABERDEEN LN
HILLSIDE LN
SOUTHSIDE RD
HAROLD LN
JOHNSON LN
MCCLURE LN
P

Fig. 2. *Buddleja davidii* (Sites 1, 2) at Ijams Nature Center, Knox County, Tennessee: **1)** Mead's Quarry at limestone kiln wall adjacent to railroad tracks (Sites 1), and **2)** Imery's Trail end near Aberdeen Lane (Site 2). [Map modified from Knoxville's Urban Wilderness, South Loop Trails: Ijams Nature Center, Ross & Mead's Quarry (Legacy Parks Foundation 2009)].

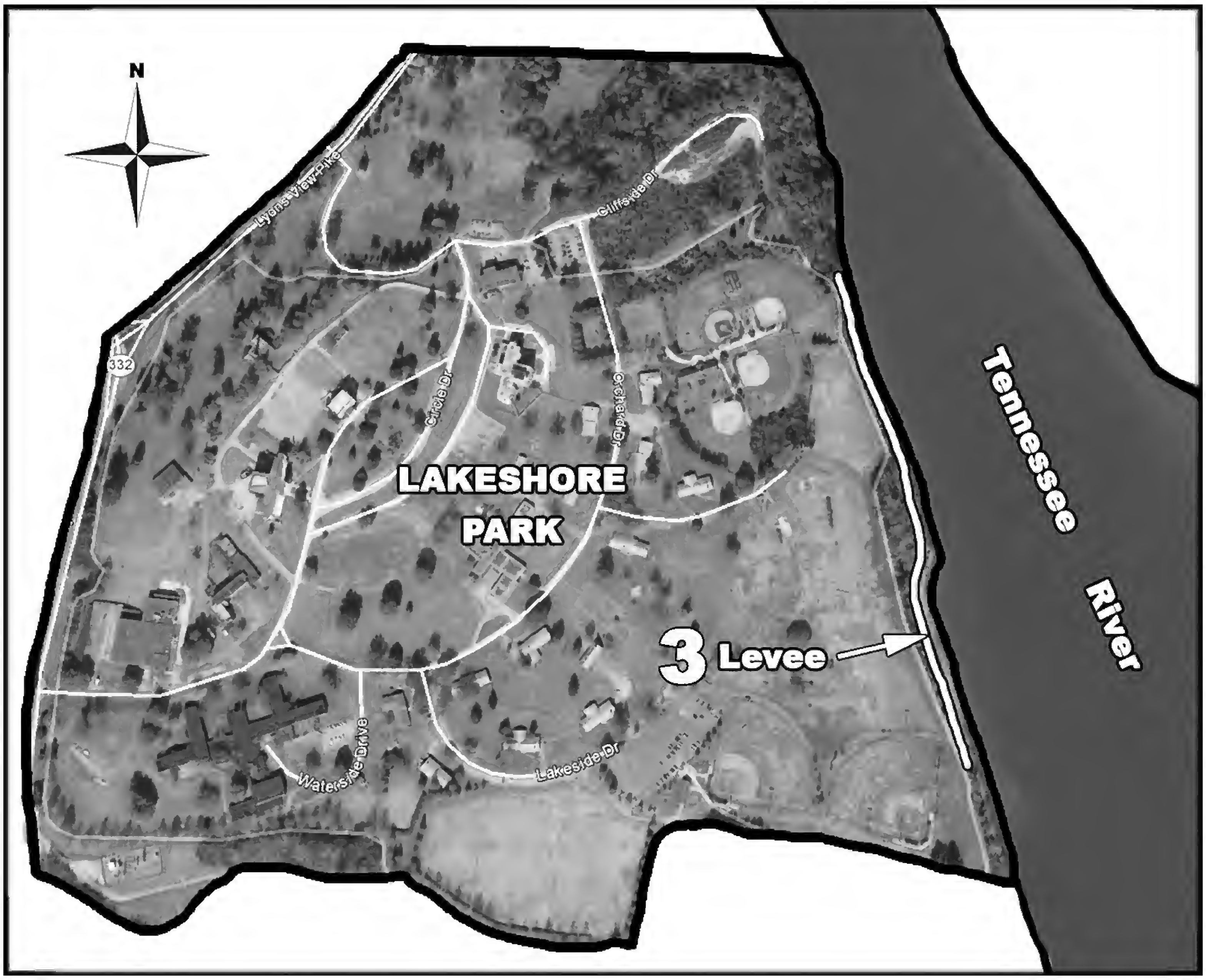

Fig. 3. Lakeshore Park levee (Site 3) designated by narrow white line adjacent to the west side of theTennessee River, Knox County, Knoxville. [Map modified from Knoxville 2013 Master Plan. (www.cityofknoxville.org/lakeshore/masterplanupdate121613.pdf)

Ijams Nature Center, a 111.3-ha (275-acre) wildlife sanctuary and wildlife environmental learning center, under the management of the Knox County Department of Parks and Recreation, Knoxville, is comprised of lands mainly from two abandoned marble quarries, Ross Quarry and Mead's Quarry (James 2010). From these two quarries, Tennessee marble, a pink to cedar-red coarse crystalline limestone rock from the Ordovician Holston Limestone Formation was excavated (James 2010). Mead's Quarry, the larger quarry, was in operation from 1881–1945 for large marble stone blocks. After 1945–1978, limestone was crushed, kiln-extracted and transported as agriculture lime for commerce by the Knoxville and Holston Railway (KXHR) K Line. Mead's Quarry Lake, a 10.1-ha (25-acre lake) subsequently was formed when water pooled in the quarry pit after Mead's Quarry closed for the last time in 1978 (Fig. 2). The KXHR railway is situated parallel to Mead's Quarry and is still in operation as a short-line spur twice a month for transporting commerce to the Tennessee River. The quarry lake and its environs became a part of Ijams Nature Center in 2001 (James 2010). In 2005, three limestone kilns were demolished with a stone wall and three lime chute openings as the only remnants today of the agricultural lime operation (Paul James, Director, Ijams Nature Center, pers. comm. 2012).

Site 1: Ijams Nature Center, Meads Quarry and Railroad Population

On November 21, 2012, a preliminary reconnaissance located the first naturalized *Buddleja davidii* population along the KXHR tracks adjacent to Mead's Quarry Lake (Site 1); 12 herbaceous and 13 woody associates were recorded (Thompson & Abbott 2013). This butterfly bush population was noted in 2003 by Dwayne Estes, Austin Peay State University, but vouchers were not taken (D. Estes, pers. comm. 2012). At this location, orange-eye butterfly bush is infrequent in relative abundance. *Buddleja davidii* consisted of 20–25 plants comprised of a few mature shrubs, smaller volunteering shrubs, and seedlings that colonized a 75 m extension of the KXHR railroad tracks parallel to the limestone wall and kiln chutes. Butterfly bushes were embedded in a thick crust of slag agriculture lime with typical seasonal vegetation cover of non-native and native woody and herbaceous species. Unseasonally late April and early May freezes in conjunction with herbicide spraying by the KXHR railway personnel between May and June 2014, killed much of the right-of-way vegetation including two adjacent large and several smaller orange-eye butterfly bushes.

The original seed source was undoubtedly derived from a few *Buddleja davidii* between the limestone kilns and the railroad tracks initially planted by a troop of Boy Scouts in 1983 as part of an ornamental planting project near Mead's Quarry (Sally Mirick, Former Director, Ijams Nature Center, pers. comm. 2012). The dispersal of the tiny wind-carried seeds has probably been partly enhanced by the "slipstreaming" wake action by the short-spur railroad freight cars and locomotives. Slipstreaming of *B. davidii* seeds was discussed in a recent descriptive study of butterfly bush dispersal, colonization, and naturalization in Kentucky (Thompson & Abbott 2013).

Twenty-seven tree, shrub, and woody vine associated species (16 native, 11 non-native) were interspersed among 68 herbaceous (28 native, 40 non-native) taxa. Mead's Quarry habitats were open, sunny, ruderal areas (hiking and biking trails, mowed and unmowed areas, parking lots, railroad track right-of-way) where many opportunistic native and non-native naturalized taxa have thrived.

The 16 native trees, shrubs, and vines were documented. Scarce native woody taxa were *Frangula caroliniana* (Walter) A. Gray and *Sambucus canadensis* L. Infrequent to occasional native woody species were *Acer negundo* L., *Celtis occidentalis* L., *Cercis canadensis* L., *Gleditsia triacanthos* L., *Juniperus virginiana* L., *Liriodendron tulipifera* L., *Parthenocissus quinquefolia* (L.) Planch., *Platanus occidentalis* L., *Rhus glabra* L., *Robinia pseudoacacia* L., *Rubus occidentalis* L., *R. pensilvanicus* Poir., *Toxicodendron radicans* (L.) Kuntze, and *Ulmus rubra* Muhl. (Table 1). Eleven naturalized woody taxa documented were infrequent *Celastrus orbiculatus* Thunb., *Ulmus pumila* L.; occasional *Ailanthus altissima* (Mill.) Swingle, *Albizia julibrissin* Durazz., *Elaeagnus umbellata* Thunb., *Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud., *Pyrus calleryana* Decne, *Rosa multiflora* Thunb ex Murray; and frequent *Ligustrum sinense* Lour., *Lonicera japonica* Thunb., *L. maackii* (Rupr.) Maxim. (Table 1). All naturalized species, except *Ulmus pumila*, are classified as woody invasives by the Tennessee Exotic Pest Plant Council (TN-EPPC 2009).

Label data from the Mead's Quarry kiln wall and railroad site, Knox County, are summarized as follows: **TENNESSEE. Knox Co.:** Knoxville, Ijams Nature Center, adjacent to Mead's Quarry Lake, between the remaining limestone kilns wall and the railroad track bed; naturalized Chinese shrubs, infrequent relative abundance, 15–30 shrubs, 35.95066°N, 83.86744°W, 272 m, 20 Nov 2012, *R.L. Thompson & K. Rivers Thompson 12-1153* (APSC, BEREA, MO, NCU, TENN); 8 Jul 2013, *R.L. Thompson & K. Rivers Thompson 13-375* (APSC, BEREA, NCU); 5 Oct 2013, *R.L. Thompson, K. Rivers Thompson, & P.F. Threadgill 13-708* (BEREA, TENN).

Site 2. Ijams Nature Center, Imery's Trail Population

On November 29, 2012, a larger second naturalized population of *Buddleja davidii* was discovered at the extreme south-southwest portion of Ijams Nature Center near the end of Imery's Trail (Site 2) near Aberdeen Lane (Fig. 2). Orange-eye butterfly bush had occasionally spread into an open sunny area where old limestone kilns and concrete block foundations were dismantled in 2008 (Paul James, Director, Ijams Nature Center, pers. comm. 2012). Butterfly bush in various phenological stages was growing among brick and concrete block debris and limestone slag wastes by Imery's Trail. The butterfly bush population was enclosed by a secondary successional mesophytic hardwood forest of frequent codominant *Acer saccharum* Marshall and *Liriodendron tulipifera* L. with a dense shrub and vine thicket. During May 2014, active bulldozing destroyed many butterfly bush shrubs when Imery's Trail to Aberdeen Lane was widened. Furthermore, the atypical late April-early May freezes caused severe die-back of butterfly bush branches.

Thirty woody associates (18 native, 12 naturalized) were recorded from this open disturbed forest edge (Table 1) scattered among 60 herbaceous (36 native, 24 non-native) taxa. Twenty-three of these woody taxa were also recorded at the Mead's Quarry (Site 1), which included frequent invasive *Ligustrum sinense*, *Lonicera* *japonica*, and *L. maackii* (Table 1). Six additional woody species (four native, two non-native) at Imery's Trail were infrequent to occasional *Campsis radicans* (L.) Seem. ex Bureau, *Clematis virginiana* L., *Euonymus fortunei* (Turcz.) Hand.-Mazz., *Fraxinus americana* L., *Pueraria montana* (Lour.) Merr. var. *lobata* (Willd.) Maesen & Almeida, and *Vitis vulpina* L. Four woody plants present at Mead's Quarry, but not recorded at Imery's Trail (Site 2) were *Frangula caroliniana*, *Gleditsia triacanthos*, *Sambucus canadensis*, and *Ulmus pumila* (Table 1). Of these 12 naturalized woody taxa, all except *U. pumila*, are listed as invasives by the TN-EPPC (2009).

The *Acer saccharum-Liriodendron tulipifera* woodland has progressed to a later seral stage of secondary succession than the Mead's Quarry site with fewer ruderal and more native herbaceous and woody taxa. The encroachment of a dense understory shrub thicket and tree canopy confines the expansion of butterfly bush colonization at the Imery's Trail site. This observation supports further the conclusions of Trueblood (2009): the migration of *Buddleja davidii*, a shade-intolerant pioneer shrub, is being controlled by competition through natural secondary plant succession.

A total of 125 herbaceous and woody associated species (91 herbaceous, 34 woody) were recorded from the two naturalized *Buddleja davidii* populations at Ijams Nature Center (Sites 1, 2). The woody species were composed of 22 native and 12 naturalized taxa. Twenty-four (14 native, 10 naturalized) of the 34 woody associates were common to both *B. davidii* population sites (Table 1). The 34 woody taxa (17 trees, 8 shrubs, 9 vines) at the two Ijams Nature Center sites were comparable to the 34 woody taxa (19 trees, 7 shrubs, 8 vines) documented at a drastically disturbed 13-year-old abandoned limestone quarry in central Kentucky (Thompson & Green 2010).

The Ijams Nature Center Imery's population (Site 2) label data are as follows: **TENNESSEE. Knox Co.:** Knoxville, Ijams Nature Center property, 230 m S of 2515 Aberdeen Lane SE beside Imery's Trail, occasional relative abundance, 60–80 naturalized shrubs among rubble, 35.94627°N, 83.87642°W, 286 m, 29 Nov 2012, *R.L. Thompson & S. Brobst 12-1160* (APSC, BEREA, MO, TENN); 8 Jul 2013, *R.L. Thompson & K. Rivers Thompson 13-376* (APSC, BEREA, BRIT, NCU, TENN); 5 Oct 2013, *R.L. Thompson, K. Rivers Thompson, & P.F. Threadgill 13-701; 13-702* (APSC, BEREA, TENN)

Site 3: Lakeshore Park Tennessee River Rip-rap Levee Population

On January 10, 2014, a third population of *Buddleja davidii* was investigated at Lakeshore Park, Knoxville, a 78.9-ha (195-acre) park also managed by the Knox County Department of Parks and Recreation. Forty-eight orange-eye butterfly bush plants occasional in relative abundance, were established on the rounded apex of a 0.53 km limestone rip-rap levee (Site 3). The levee adjoins Lakeshore Park on the riparian west shoreline of the Tennessee River, 17.2 km downstream from Ijams Nature Center (Fig. 3). Orange-eye butterfly bush colonization on the levee was probably due to the combination of wind-and-water seed dispersal. Twenty-eight woody associates (17 native, 11 non-native) were documented. Infrequent to occasional associated species on the levee crest were *Ailanthus altissima*, *Albizia julibrissin*, *Ligustrum sinense*, *Lonicera maackii*, *Paulownia tomentosa*, *Platanus occidentalis*, *Rosa multiflora*, and *Salix nigra* Marshall. Eight woody associates (7 native, 1 non-native) not present at Ijams Nature Center (Sites 1, 2) were the infrequent *Acer saccharinum* L., *Carya cordiformis* (Wangenh.) K. Koch, *Cornus amomum* Mill., *Euonymus pungens* Thunb., *Fraxinus pennsylvanica* Marshall, *Quercus muhlenbergii* Engelm., *Salix nigra*, and *Ulmus americana* L. (Table 1).

Label data for Lakeshore Park (Site 4), Knoxville are as follows: **TENNESSEE. Knox Co.:** Knoxville, Lakeshore Park, along the top of a limestone boulder rip-rap levee, 48 naturalized shrubs, occasional relative abundance, 35.92372°N, 83.98660°W, 253 m at apex, 249 m at shoreline, 10 Jan 2014, *R.L. Thompson & D.M. Bruce 14-02* (APSC, BEREA, TENN).

Buddleja davidii naturalized in Anderson County

Orange-eye butterfly bush was documented from two naturalized populations in Anderson County on April 5, 2014. Both population sites are entirely located within the Southern Limestone/Dolomite Valleys and Low Rolling Hills Ecoregion within the Ridge and Valley Province of potential Appalachian Oak and Mesophytic Forest (Griffith et al. 1997).

Site 4: Grassy Road Shoulder and Highwall Population

A *Buddleja davidii* population was situated within the city limits of Clinton, Tennessee, beside the Charles G. Seivers Boulevard (TN 61W). A mature butterfly bush, 4 m x 3 m, was growing within a mixed tall fescue (*Fes-*

tuca arundinacea Schreb.) road shoulder adjacent to an Ordovician limestone highwall road cut (Site 4). This single shrub has undoubtedly served as the seed source to the 8–9 scarce volunteering shrubs embedded within limestone fractures of a 7–9 m vertical highwall.

Twenty-one woody associates (10 native, 11 non-native) on the road shoulder and highwall were recorded (Table 1). No new native or non-native woody taxa were recorded for Site 4. Among 11 state-listed invasive species, *Ligustrum sinense* and *Lonicera maackii* were frequent codominant shrubs. The unusual freezes of late April and early May killed most of the new leafing branches of the large "parent" butterfly bush, and three small butterfly bushes embedded in the limestone highwall crevices died from the spring freezes as well. Little or no freeze effects were noted on the 11 invasive taxa. Some root collar sprouting was evident on May 18, 2014, and by late June and July, lilac-lavender inflorescences appeared on the surviving parent and surviving highwall plants. Senescence occurred by late September.

Label data for the Anderson County roadside and highwall (Site 4) are as follows: **TENNESSEE. Anderson Co.:** Clinton, TN 61 W adjacent to Clinch River, tall fescue road shoulder between limestone highwall talus, scarce relative abundance, ca. 8–9 small shrubs established in crevices of a 5–7 m highwall from a large parent shrub, infrequent relative abundance, 36.08231°N, 84.161154°W, 211 m, 5 Apr 2014, *R.L. Thompson & D.R. Bruce 14-23* (APSC, BEREA, TENN); severe leaf frost damage, 18 May 2014, *R.L. Thompson & K. Rivers Thompson 14-111* (BEREA, TENN); lilac-lavender flowers on new or undamaged branches of parent shrub, 21 Aug 2014, *R.L. Thompson & G.N. Douglas 14-520* (APSC, BEREA, TENN).

Site 5: Abandoned Asphalt, Concrete, and Gravel Landfill

The second Anderson County population was located in Oak Ridge east of Southern Illinois Avenue (TN 62) on Union Valley Road contiguous to the east side of the Oak Ridge Golf Center, 119 Union Valley Road (Site 5). Two rare orange-eye butterfly bushes were growing in different areas 40 m apart in an open, nearly level abandoned asphalt, concrete, and aggregate gravel landfill. A smaller shrub had only a single shoot regenerating from the rootstock, while a second larger shrub had several basal shoots rejuvenating from the rootstock although most of the shrub branches exhibited severe dieback.

This abandoned landfill (Site 5) had the highest species richness of the seven sites with 34 associated woody plants (20 native, 14 non-native) within the immediate vicinity of these two shrubs (Table 1). This landfill ruderal habitat site promoted wide-spread seed dispersal and establishment of both native and non-native woody taxa from various anthropogenic refuse sources. *Ligustrum sinense*, *Lonicera japonica*, *L. maackii*, and *Pyrus calleryana* were the frequent dominant taxa. Three additional native taxa at the landfill site not present at the other four sites were occasional in relative abundance: *Ampelopsis cordata* Michx., *Fraxinus pennsylvanica* Marshall, and *Rhus copallinum* L. Four non-native scarce naturalized taxa present were *Morus alba* L., *Nandina domestica* Thunb., *Prunus persica* (L.) Batsch, and *Yucca filamentosa* L. (Table 1).

Label data for the abandoned landfill (Site 5) in Anderson County are as follows: **TENNESSEE. Anderson Co.:** Oak Ridge, Oak Ridge Highway (TN 170) to Southern Illinois Avenue (TN 62) to Union Valley Road east to a disused city landfill adjacent to Oak Ridge Golf Center, 119 Union Valley Road, rare relative abundance, small solitary shrub embedded in fractured asphalt-concrete layer, 36.00203°N, 84.22006°W, 284 m, 5 Apr 2014, *R.L. Thompson & D.R. Bruce 14-24* (APSC, BEREA, TENN); small shrub with a single surviving basal branch and lilac-lavender flowers, 21 Aug 2014, *R.L. Thompson & G.N. Douglas 14-537* (BEREA); larger shrub with lilac-lavender inflorescences from several basal shoots from rootstock, remainder of shrub dead, 36.00166°N, 84.21981°W, 282 m, 21 Aug 2014, *R.L. Thompson & G.N. Douglas 14-538* (APSC, BEREA, TENN).

Buddleja davidii naturalized in DeKalb County

On April 15, 2014, a naturalized population of *Buddleja davidii* was discovered off TN 83 north of Smithville to Holmes Creek Road for 3.8 km north across from the concrete remains of Hidden Harbor Marina at Center Hill Lake. The abandoned roadside thicket (Site 6) is located entirely within the Outer Nashville Basin Ecoregion of the Interior Plateau Province. Major vegetation is comprised of Oak-Hickory Forest (Griffith et al. 1997).

Site 6: Abandoned Gravel Road by Center Hill Lake

A total of 9–12 infrequent seed-producing shrubs in various growth stages were rooted in scattered limestone aggregate near an exposed herbicide-sprayed power line cut. Twenty-two woody associates (14 native, 8 naturalized) were recorded at Site 6 (Table 1). This population of orange-eye butterfly bush has been heavily shaded by the dense forest edge thicket by the frequent Asian invasives, *Ligustrum sinense*, *L. vulgare* L., and *Lonicera maackii* (Table 1). The health of the butterfly bush population was also severely affected by late April and early May freezes with a majority of the larger shrub branches killed back to the rootstock. Likewise, this population appeared to be restricted to the abandoned gravel road due to herbicide spraying of the nearby power line corridor.

Label data at the DeKalb County disused roadside thicket (Site 6) are as follows: **TENNESSEE. DeKalb Co.:** Smithville, on Holmes Creek Road, 3.8 km N of TN 83 along Center Hill Lake on an abandoned limestone aggregate road near power line cut near the Hidden Harbor Marina foundation, scarce relative abundance, ca. 9–10 shrubs present, 36.700175°N, 85.26480°W, 203 m, 15 Apr 2014, *R.L. Thompson & S.J. Stedman 14-26* (APSU, BEREA, TENN); lilac-rose flowers, severe die-back from spring freezes, 11 Jul 2014, *R.L. Thompson & G.N. Douglas 14-330* (APSU, BEREA, TENN)

Buddleja davidii naturalized in Davidson County

Shelby Park, a 136-ha (336-acre) urban multi-use park located in downtown Nashville adjacent to the Cumberland River, is located in Davidson County (Nashville Parks & Recreation 2014). The city park lies entirely within the Outer Nashville Basin Ecoregion of the Interior Plateau Province and consists of potential Oak-Hickory Forest (Griffith et al. 1997).

Site 7: Steep Cumberland River Rip-rap Bank Population

Two mature *Buddleja davidii* shrubs were growing out of large limestone rip-rap along the steep embankment thicket of the Cumberland River (Site 7) near a chain link fence separating the Shelby Park lawn from Davidson Street (Music City Bikeway). The thyrsoid inflorescence was composed of lilac-lavender perfect, 4-merous flowers (Fig. 4) as all *B. davidii* shrubs were within the seven populations. Twenty-four woody associates (17 native, 7 naturalized) were recorded from this Cumberland River riparian thicket (Table 1). The two butterfly bushes were totally surrounded by a dense thicket of *Euonymus fortunei*, *Ligustrum sinense, Lonicera japonica*, *L. maackii,* and various occasional native woody vines, *Ampelopsis cordata*, *Parthenocissus quinquefolia, Toxicodendron radicans*, and *Vitis vulpina*. Two additional rare native species reported for the seven sites were *Catalpa bignonioides* Walter and *Smilax rotundifolia* L. (Table 1). Frost damage was not evident mainly due to the temperature buffer from the close proximity to the Cumberland River. No seedlings or evidence of butterfly bush colonization were found.

Label data for these two shrubs on the bank of the Cumberland River are as follows: **TENNESSEE. Davidson Co.:** Nashville, Shelby Park, Davidson Street (Music City Bikeway) across chain link fence on a steep open embankment in limestone rip-rap by Cumberland River; rare relative abundance, first naturalized shrub, 36.16505°N, 86.73046°W, 130 m, 16 Apr 2014, *R.L. Thompson 14-30* (APSC, BEREA, MO, TENN); lilac-lavender flowers, slight branch frost damage, 11 Jul 2014, *R.L. Thompson & G.N. Douglas 14-336* (APSU, BEREA, TENN); second shrub adjacent lower down, lilac-lavender inflorescence, 36.164972°N, 86.73070°W, 129 m, 11 Jul 2014, *R.L. Thompson & G.N. Douglas 14-338* (BEREA, TENN).

Synopsis of Naturalized *Buddleja davidii* Populations and Woody Associates

Buddleja davidii was documented as locally naturalized from field reconnaissance at seven population sites in four Tennessee counties as follows: Knox (3), Anderson (2), DeKalb (1), and Davidson (1) during 2012–2014 (Table 1).

Ruderal or culturally disturbed sites and relative abundance values for the seven *B. davidii* populations were as follows: Knox County, Ijams Mead's Quarry Railroad (Site 1) = Scarce; Knox County, Ijams Imery's Trail (Site 2) = Occasional; Knox County, Lakeshore Park Rip-rap Levee, Tennessee River (Site 3) = Occasional; Anderson County, Highway Road Shoulder and Highwall (Site 4) = Scarce; Anderson County Disused Landfill (Site 5) = Rare; DeKalb County, Abandoned Road Thicket at Center Hill Lake (Site 6) = Infrequent; and Davidson County, Cumberland River rip-rap embankment (Site 7) = Rare. These naturalized *B. davidii* populations locally confined to culturally-derived and disturbed habitats have not volunteered or colonized any natural thickets or forest edges.

A summary of descriptive site characteristics and woody associated species from the seven *B. davidii* population studies include the following:

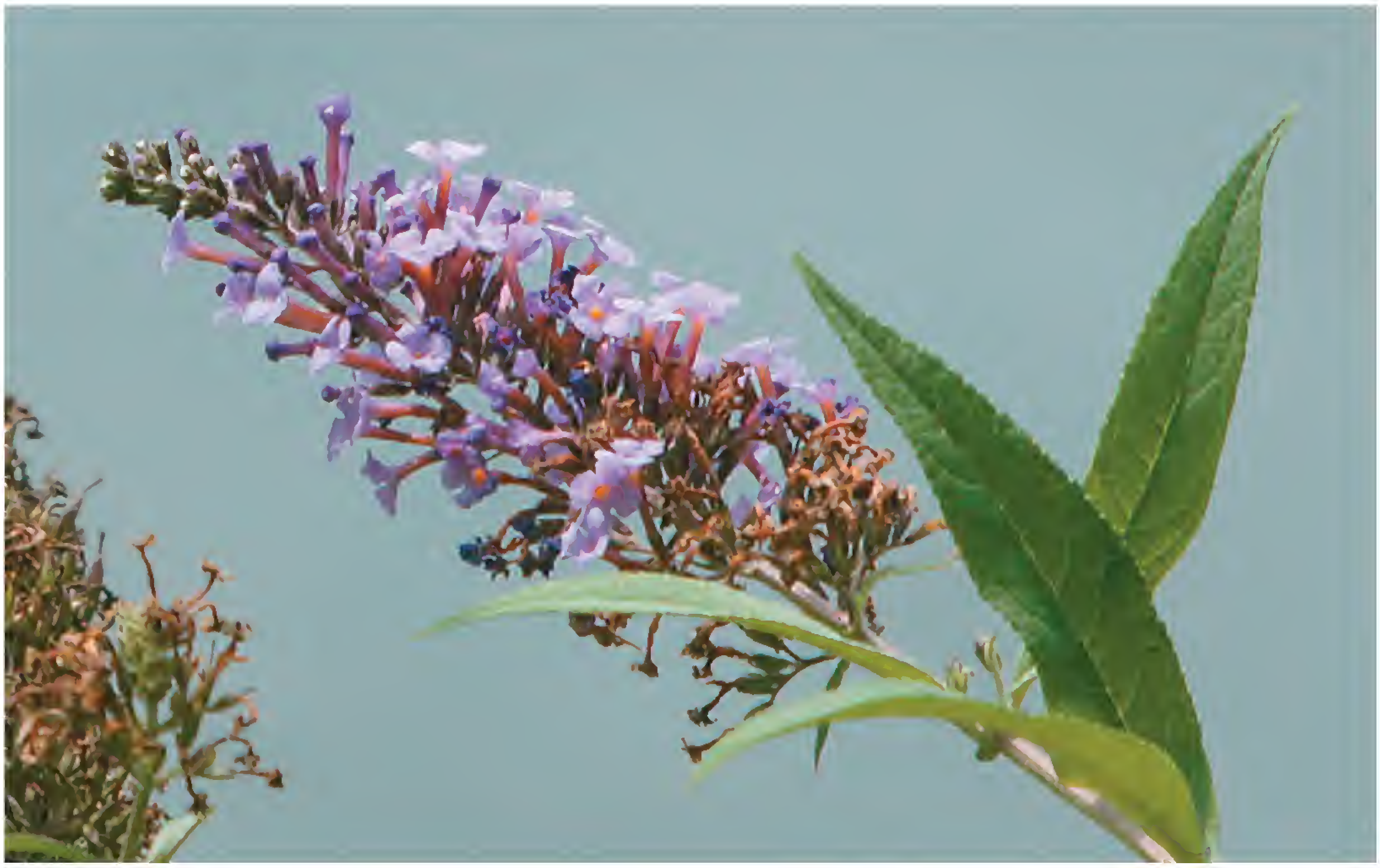

Fig. 4. ***Buddleja davidii*** **inflorescence of lilac-lavender perfect flowers from Cumberland River rip-rap embankment population (Site 7), by Shelby Park, Nashville. (Photo taken by Michael R. Smith, 8 July 2013).**

1) Fifty-one woody species [32 native (62.75%), 19 non-native (37.25%)] in 41 genera from 26 plant families were documented among the study sites.

2) These 51 woody taxa consisted of 26 trees (19 native, 7 exotic), 14 shrubs (7 native, 7 exotic), and 11 woody vines (7 native, 4 exotic).

3) Fifteen invasives of the 19 naturalized woody taxa (78.95%) classified by the Tennessee Exotic Pest Plant Council (TN-EPPC 2009) are listed as follows: Severe Threat (10), Significant Threat (2), Lesser threat (1), and Alert (2).

4) Eleven woody non-native invasives with a Relative Frequency (frequency of occurrence) of 57% or greater (4 of 7 sites) are listed in order: *Ailanthus altissima, Ligustrum sinense, Lonicera japonica, L. maackii, Albizia julibrissin, Pyrus calleryana, Celastrus orbiculatus, Paulownia tomentosa, Rosa multiflora, Elaeagnus umbellata,* and *Euonymus fortunei* (Table 1).

5) These 11 opportunistic woody invasives are inclined to have a greater ecological amplitude and tolerance to volunteer, colonize, compete, thrive, and invade natural habitats in early seral stages of progressive secondary succession than *Buddleja davidii.*

6) Most of these invasives have greater relative abundance values than *Buddleja davidii* populations.

7) Some non-native invasive adaptations include direct and indirect insolation, variation in moisture-soil requirements and varied pH, strong intraspecific and interspecific competition, better acclimation to cold and herbicides, and a length of establishment over 10 years in the case of typical woody non-native species (Pyšek et al. 2004).

8) No Tennessee special concern, threatened, or endangered herbaceous or woody taxa on the Rare Plant List (Crabtree 2014) were recorded within or near proximity to the seven study sites.

CONCLUSION

We determined *Buddleja davidii* to be locally naturalized in Tennessee based on observations from field reconnaissance, voucher documentation from extant populations in Knox, Anderson, DeKalb, and Davidson counties, and by label information from examination of Tennessee herbarium specimens from Cumberland, Hamilton, and Washington counties. *Buddleja davidii* definitely did not exhibit the widespread invasive adaptations displayed by most non-native woody invasives in this study. Butterfly bush relative abundance values for the seven populations ranged from rare, scarce, infrequent, to occasional. These seven populations have not expanded their range beyond ruderal and culturally-derived areas. At an optimal classification, *B. davidii* populations observed in this study are sparingly and locally naturalized. Similarly in a Kentucky study, *Buddleja davidii* was reported naturalized, but was not determined to be invasive (Thompson & Abbott 2013).

As observed from this study, *Buddleja davidii* is a shade intolerant, short-lived pioneer species established in ruderal habitats of Tennessee that is eliminated through natural plant succession in absence of disturbance. Butterfly bush continues to be restricted to those disturbed habitats rather than secondary forested areas. Other contributing factors observed toward limited naturalization include poor competition among native and especially aggressive invasive woody taxa, low adaptability to unseasonably cold temperatures, and a high sensitivity to herbicides.

Trueblood (2009) evaluated the impact of *Buddleja davidii* on natural vegetation in North Carolina and reported that it has a tendency to be eliminated through natural plant succession. Moreover, orange-eye butterfly bush exhibited little ecological impact, distribution expansion, or invasive potential. These premises also appear to be applicable to Tennessee and Kentucky naturalized *B. davidii* populations. We propose the limited naturalization of *Buddleja davidii* in Tennessee at this present time clearly does not imply any invasive status beyond its current "Alert" rank from the TN-EPPC (2009). Exotic pest plant council personnel in Tennessee, Kentucky, and other southeastern states could benefit from evaluating *B. davidii* with a rational assessment system, such as developed for North Carolina.

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JOURNAL NOTICE

Ashok Gadgil & Diana M. Liverman. 2014 (Oct). **Annual Review of Environment and Resources, Volume 39.** (ISSN: 1543-5938; ISBN: 978-0-8243-2339-4, hbk). Annual Reviews, Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303, U.S.A. (**Orders:** www.AnnualReviews.org, science@annualreviews.org, 1-800-523-8635, 1-650-493-4400). $90.00, 688 pp., 7 ⅝" × 9 ⅜".

ABOUT THIS JOURNAL—The *Annual Review of Environment and Resources,* in publication since 1976, provides authoritative reviews of significant topics within environmental science and engineering, including ecology and conservation science, water and energy resources, atmosphere, oceans, climate change, agriculture and living resources, and human dimensions of resource use and global change.

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ADDENDUM TO THE VASCULAR FLORA OF THE HANCOCK BIOLOGICAL STATION, MURRAY STATE UNIVERSITY, CALLOWAY COUNTY, KENTUCKY, U.S.A.

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ABSTRACT

A vascular plant reconnaissance was conducted at the Hancock Biological Station (HBS) of Murray State University during the summers of 2012–2015. The HBS a 37.5-ha tract of mainly upland oak-hickory forest, is located 23 km from Murray, Kentucky, in northeastern Calloway County within the Jackson Purchase Region. In 2007, a floristic study of HBS reported 573 specific and infraspecific taxa in 334 genera from 121 families. Twenty-one additional taxa (12 native, 9 non-native) have been documented from incidental collections. Thirteen taxa were new Calloway County distribution records including five Kentucky-listed invasive species. *Ulmus alata* was also documented as a new host tree for *Phoradendron leucarpum* ssp. *leucarpum* in Calloway County. The documented native and exotic flora of HBS presently consists of 594 taxa, 345 genera, and 126 families.

Key Words: Hancock Biological Station, Calloway County, invasive plants, Kentucky vascular flora

RESUMEN

Un reconocimiento de plantas vasculares se llevó a cabo en la Estación Biológica Hancock (HBS) de la Universidad Estatal de Murray durante los veranos de 2012 a 2015. El HBS, un tramo de 37,5 hectáreas principalmente de bosque de roble-nogal de tierras altas, se encuentra a 23 km de Murray, Kentucky, en el noreste del Condado de Calloway en la Región Compra Jackson. En 2007, un estudio florístico de HBS reportó 573 taxones específicos e infraespecíficos de 334 géneros de 121 familias. Veintiún nuevos taxones (12 nativos, 9 no nativos) han sido documentados en colecciones incidentales. Trece taxones fueron nuevos registros de distribución del Condado de Calloway, incluyendo cinco especies invasoras listadas en Kentucky. *Ulmus alata* también fue documentado como un nuevo árbol huésped de *Phoradendron leucarpum* ssp. *leucarpum* en el Condado de Calloway. La flora nativa y exótica documentada de HBS actualmente consta de 594 taxones, 345 géneros y 126 familias.

Hancock Biological Station (HBS) was founded in 1966 by Hunter M. Hancock, Professor of Biology at Murray State University from a 16.2-ha tract of old fields, pastures, and secondary successional upland oak-hickory forest in northeastern Calloway County (White 2002). The HBS now consists of a 37.5-ha tract that adjoins Kenlake State Resort Park to the north, impounded Kentucky Lake shoreline of the Tennessee River on the east, and Pacer Point to the southeast off Watersport Road. The HBS is located 24 km from Murray, the county seat of Calloway County, the southeastern-most county of the eight county Jackson Purchase Region.

Thompson (2003) recorded 560 taxa in 320 genera from 110 families from 1998–2002 in a checklist of the vascular plants of HBS. Thompson (2007) designated 10 habitats at HBS in an on-going floristic study conducted during the summers of 2003–2006. Forest vegetation is predominately upland stands of dry or dry-mesic oak-hickory forest, and mid-successional oak-hickory woodlands, which border various culturally derived ruderal areas, wetland habitats, and an old field burnt warm-season restored prairie. Thompson (2007) reported the known vascular flora from Hancock Biological Station as 573 specific and infraspecific taxa, 334 genera, and 121 families. Woods and Fuller (1988) listed 1018 taxa, 462 genera, and 129 families for the vascular flora of Calloway County.

In conjunction with teaching an undergraduate/graduate field botany course at HBS during the summers of 2012–2015, we conducted a floristic reconnaissance within the boundaries of HBS and collected representa-

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tive vouchers for taxa new to the station. Several newly discovered plants have volunteered and colonized existing HBS habitats since the 2007 survey report.

Nomenclature and classification follow Jones (2005), with three exceptions that reflect recent familial recircumscriptions, i.e., *Paulownia* is transferred from Bignoniaceae to Paulowniaceae, *Mazus* from Scrophulariaceae to Mazaceae, and *Celtis* from Ulmaceae to Cannabaceae (Stevens 2001). Herbarium acronyms follow *Index Herbariorum* from Thiers (2014), i.e., Berea College Herbarium (BEREA), University of Florida Herbarium (FLAS), and Murray State University Herbarium (MUR). This addendum to the HBS annotated list mainly follows the format of Thompson (2007). Symbols preceding the scientific name of a taxon may include: an asterisk (*) for a non-native taxon; a double asterisk (**) for a state-listed invasive species by the KY-EPPC (2013); a dagger (†) for a native or exotic planted taxon; and a diesis (‡) for a Calloway County distribution record based on the maps of Campbell and Medley (2012) and USDA, NRCS (2014). Relative abundance values are abbreviated as Rare (R); Scarce (S); Infrequent (I); Occasional (O); Frequent (F); and Abundant (A)

ALISMATACEAE

Echinodorus cordifolius (L.) Griseb., Creeping Burhead, emergent at Kentucky Lake shoreline east of Watersport Road; R. Associate: *Carex crus-corvi*; 27 Jun 2014, *J.R. Abbott & R.L. Thompson 26525* (BEREA). This was in very young bud when found and was transplanted to await flowering. The original inflorescence died, but the plant reflowered and was pressed 20 Aug 2014.

ASTERACEAE

‡**Senecio vulgaris* L., Common Groundsel, aggregate gravel at the side border of the Mesocosm Building; R, 30 Jun 2013, *R.L. Thompson & J.R. Abbott 13-252* (BEREA). Campbell and Medley (2012) mapped six Kentucky counties for this European annual weed.

CANNABACEAE

Celtis laevigata Willd., Sugarberry, throughout oak-hickory forest near Kentucky Lake; F, 20 Jun 2013, *R.L. Thompson & J.R. Abbott 13-325* (BEREA, FLAS, MUR). The key features used for differentiating *Celtis laevigata* and *C. occidentalis* L., vary from author to author, e.g., Jones (2005), Whittemore (2013). Species circumscription, obviously, involves taxonomic judgment, and the treatment provided by Alan Whittemore in the *Flora of Missouri* seems to be the best for reflecting biological reality in the landscape. Thus, many of the plants traditionally seen as *C. occidentalis* at HBS are now understood to be *C. laevigata*.

CARYOPHYLLACEAE

‡*Sagina decumbens* (Elliott) Torrey & A. Gray, Trailing Pearlwort, wet lawn beside three 1200-gallon stock water tanks; S. Associates: *Callitriche terrestris, Centunculus minimus, Isolepis carinata*; 5 Jun 2013, *R.L. Thompson & J.R. Abbott 13-261* (BEREA, MUR). Campbell and Medley (2012) mapped five counties for this often overlooked taxon; the USDA, NRCS (2014) mapped 10 Kentucky counties.

CELASTRACEAE

‡***Celastrus orbiculatus* Thunb., Oriental bittersweet, dry-oak-hickory forest ecotone at back of Resource Building, a severe threat invasive colonizer; R, 5 Jun 2012, *R.L. Thompson 12-653* (BEREA); roadside edge of woods, S side of Emma Road W of junction with Wolfson Road, 28 Jun 2014, *J.R. Abbott 26527* (FLAS).

CORNACEAE

†**Cornus kousa* F. Buerger ex Miq., Pagoda Dogwood, an introduced Asian tree persisting as an ornamental in lawn at the front of the Resource Building; R, 26 Jun 2013, *R.L. Thompson & J.R. Abbott 13-253* (BEREA, MUR).

CYPERACEAE

‡*Carex crus-corvi* Shuttlew. ex Kunze, Crowfoot Sedge, emergent at Kentucky Lake shoreline east of Watersport Road; R. Associate: *Echinodorus cordifolius*; 27 Jun 2014, *R.L. Thompson & J.R. Abbott 14-248* (BEREA, FLAS, MUR).

HYDROCHARITACEAE

‡***Hydrilla verticillata* (L.f.) Royle, Hydrilla, an Old World submergent in Kentucky Lake near HBS Boat Dock; R, 27 Jun 2013, *R.L. Thompson & J.R. Abbott 13-341* (BEREA, MUR). Jones (2005) did not list *Hydrilla verticillata* as a current taxon for Kentucky. Campbell and Medley (2012) mapped only Jefferson and Trigg counties; USDA, NRCS (2014) noted Floyd, Jefferson, Johnson, Knott, and Trigg counties.

LENTIBULARIACEAE

‡*Utricularia gibba* L., Longspur Creeping Bladderwort, submergent in 14 year-old pond; I. Associate: *Potamogeton nodosus*; 27 Jun 2014, *R.L. Thompson & J.R. Abbott 14-251* (BEREA, FLAS, MUR).

MAGNOLIACEAE

†*Magnolia grandiflora* L., Southern Magnolia, a planted native tree persisting as an ornamental in lawn circle near Main Building; R, 25 Jun 2013, *R.L. Thompson & J.R. Abbott 13-252* (BEREA, MUR).

MAZACEAE

‡**Mazus pumilus* (Bernm. f.) Steenis, Japanese Mazus, near rail fence in front lawn of Main Building; R, 2 Jun 2013, *R.L. Thompson & J.R. Abbott 13-257* (BEREA, MUR). We also documented this often passed over European taxon at the Land Between The Lakes as a distribution record for Lyon County at the Woodlands Nature Center, 19 Jun 2013, *R.L. Thompson & J.R. Abbott 13-310* (BEREA). Campbell and Medley (2012) mapped Jefferson, Lewis, and McCracken counties; the USDA, NRCS (2014) listed Fayette, Henderson, Jefferson, Lewis, and McCracken counties.

MORACEAE

‡**Fatoua villosa* (Thunb.) Nakai, Mulberry Weed, wet gravel floor inside of Greenhouse Building; O, 5 Jun 2012, *R.L. Thompson 12-656* (BEREA); 2 Jun 2013, *R.L. Thompson & J.R. Abbott 13-251* (BEREA, FLAS, MUR). Campbell and Medley (2012) mapped six Kentucky counties mainly from voucher specimens reported by Vincent (2004). The USDA, NRCS (2014) mapped seven Kentucky counties.

OPHIOGLOSSACEAE

Ophioglossum pycnostichum (Fern.) A. & D. Löve, Southern Adder's-tongue, 22 plants (6 fertile) found along an off-trail mesic drainage area below Dry-Mesic Oak-Hickory Forest. Associates: *Botrychium dissectum, Carex grayi, Chasmanthium latifolium, Dioscorea villosa, Polystichum acrostichoides, Trepocarpus aethusae*; I, 5 Jun 2015, *J.R. Abbott 26814* (BEREA). Woods and Fuller (1988) first reported this fern from Calloway County based on *Hunter 803* (MUR).

OXALIDACEAE

Oxalis dillenii Jacq., Southern Yellow Wood Sorrel, scattered in mowed and unmowed lawn; O, 2 Jun 2013, *R.L. Thompson & J.R. Abbott 13-361* (BEREA, MUR).

PAULOWNIACEAE

***Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud., Chinese Empress Tree, along trail in oak-hickory forest ecotone, a recent Asian colonizer at HBS; S, 20 Jun 2013, *R.L. Thompson & J.R. Abbott 13-328* (BEREA, MUR); 27 Jun 2014, *R.L. Thompson & J.R. Abbott 14-253* (BEREA). One sapling in a large water tank (dried out with terrestrial vegetation) and two seedlings were in gravel adjacent to the Resources Building, 13 Jun 2014, *J.R. Abbott 26480* (FLAS).

POACEAE

Dichanthelium scoparium (Lam.) Gould, Velvety Panic Grass, seasonally wet ditch at Emma Drive east of entrance gate; S, 5 Jun 2012, *R.L. Thompson 12-654* (BEREA); 25 Jun 2012, *R.L. Thompson & J.R. Abbott 12-791* (BEREA, MUR).

‡**Vulpia myuros*(L.) C.C. Gmel, Rat-tail Fescue, gravel along roadside and around stock water tanks on W side of Greenhouse Building, S. Associates: *Acalypha rhomboidea, Conyza canadensis, Euphorbia maculata*; 12 Jun 2015, *R.L. Thompson & J.R. Abbott 15-403* (BEREA). A naturalized European annual reported in six Kentucky counties by Campbell and Medley (2012) and USDA, NRCS (2014).

POTAMOGETONACEAE

‡*Potamogeton nodosus* Poiret, Leafy Pondweed, floating-leaved aquatic in 14 year-old pond; F. Associate: *Utricularia gibba*; 25 Jun 2012, *R.L. Thompson & J.R. Abbott 12-815* (BEREA, MUR); 27 Jun 2014, *R.L. Thompson & J.R. Abbott 14-250* (BEREA, FLAS).

PRIMULACEAE

‡*Centunculus minimus* L., Chaffweed, wet lawn beside three 1200 gallon stock water tanks; O, 5 Jun 2013, *R.L. Thompson & J.R. Abbott 13-260* (BEREA, MUR). Abbott et al. (2001) documented the first Kentucky collection in Madison County [*R.L. Thompson & J.R. Abbott 95-374* (BEREA)] since 1840 [*Short s.n.* (PH)] in Muhlenberg County. Campbell and Medley (2012) also mapped Harlan County. The USDA, NRCS (2014) listed Harlan, Madison, and Muhlenberg counties.

‡***Lysimachia nummularia* L., Moneywort, Kentucky Lake shoreline; O, 20 Jun 2013, *R.L. Thompson & J.R. Abbott 13-327* (BEREA, MUR).

VISCACEAE

Phoradendron leucarpum (Raf.) Rev. & Johnst. ssp. *leucarpum*, American Mistletoe, a single clump hemiparasitic in *Ulmus alata* diagonally from Wolfson Drive off Emma Drive, a new host tree for Calloway County; R, 30 Mar 2013, *R.L. Thompson & W.W. Overbeck 13-20* (BEREA, MUR). Thompson and McKinney (1990) first reported *Ulmus alata* as a mistletoe host tree for Kentucky in Lyon and Trigg counties at Land Between The Lakes. Thompson (2007) previously documented mistletoe on *Carya glabra* in dry oak-hickory forest at HBS [13 Oct 2006, *R.L. Thompson & M.K. Graves 06-757* (BEREA, MUR)]. Campbell and Medley (2012) mapped mistletoe for Calloway County based upon the above 2006 collection.

VITACEAE

Vitis vulpina L., Frost Grape, in an oak-hickory woodland ecotone; I, 27 Jun 2014, *R.L. Thompson & J.R. Abbott 14-252* (BEREA, MUR); also in shrub thicket at woodland edge W of the Mesocosm Building and observed at three other scattered woodland sites, 4 Jun 2014, *J.R. Abbott 26470* (FLAS).

We documented an additional 21 vascular plant species, 11 genera, and five families for the flora of Hancock Biological Station. These 21 species (12 native and 9 non-native) comprise 13 new distribution records for Calloway County. Five are listed as Kentucky state-listed invasive plants by the KY-EPPC (2013). The 594 taxa account for 58.3% of the 1018 species listed by Woods and Fuller (1988) for the flora of Calloway County.

The documented vascular plants of the Hancock Biological Station now consist of 594 plant species, 345 genera, and 126 families. These 594 taxa account for nearly 23% of the 2600 recorded by Jones (2005) for the Commonwealth of Kentucky. Concentrated collecting still needs to be conducted for additional vascular plants in western Kentucky as 13 of 21 taxa were new Calloway County distribution records.

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BOOKS RECEIVED

Marco Madella, Carla Lancelotti, & Manon Savard. 2014. **Ancient Plants and People: Contemporary Trends in Archaeobotany.** (ISBN-13: 978-0-8165-2710-6, hbk). The University of Arizona Press, Main Library Building, 5th Floor, 1510 E. University Blvd., P.O. Box 210055, Tuscon, Arizona 85721-0055, U.S.A. (**Orders:** www.uapress.arizona.edu, 1-800-621-2736). $70.00 US, 344 pp., 6" × 9".

Amy Eisenberg. 2013. **Aymara Indian Perspectives on Development in the Andes.** (ISBN-13: 978-0-8173-1791-1, cloth). The University of Alabama Press, Box 870380, Tuscaloosa, Alabama 35487-0380, U.S.A. (**Orders:** www.uapress.ua.edu, 1-800-621-2736). $49.95 US, 38 illustrations, 280 pp., 6 ¼" × 9 ¼".

Wilhelm Barthlott, Kerstin Burstedde, Jan Laurens Geffert, Pierre L. Ibisch, Nadja Korotkova, Andrea Miebach, M. Daud Rafiqpoor, Anke Stein, & Jens Mutke. 2015. **Biogeography and Biodiversity of Cacti.** Schumannia 7. (ISSN: 1437-2517; ISBN-13: 978-3-7308-1144-3, hbk). Deutschen Kakteen-Gesellschaft e.V. und der Gesellschaft Österreichischer Kakteenfreunde (German Cactus Society and the Austrian Cactus Friends). (**Orders:** www.dkg.eu, gs@dkg.eu). 205 pp., color figures and maps, English-German text, 8 ½" × 12".

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FLORISTICS AND COMMUNITY ECOLOGY OF AQUATIC VEGETATION OCCURRING IN SEVEN LARGE SPRINGS AT OZARK NATIONAL SCENIC RIVERWAYS, MISSOURI (U.S.A.), 2007–2012

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ABSTRACT

We studied the aquatic vegetation communities of seven large springs located at Ozark National Scenic Riverways, Missouri, 2007–2012. This study provides a baseline for assessing the impacts of anthropogenic and natural disturbances on the ecological integrity of springs. Vegetation was assessed quantitatively along sample cells located on multiple transects in each spring. We list 69 distinct taxa with substantial overlap of species occurrences among springs, including 6 families, 6 genera, and 6 species of algae, and 9 families, 12 genera, and 19 species of mosses and liverworts. Among angiosperms, we report 10 families, 13 genera, and 20 species of monocots, and 16 families, 23 genera, and 24 species of dicots. Some species previously reported from the springs are no longer present, which may be due to long-term changes in watershed condition. Individual sample cells typically contained four to six taxa, although Welch Spring generally had only two to three taxa represented. Effective numbers of species were generally consistent among years for all springs, but the various species did not occur in equal abundance in the community within or among sample years. Taxa richness was slightly higher than Simpson's Diversity Index effective number (De) and Shannon's Diversity Index effective number (He) for all years among springs. He ranged from 1.34 to 3.76 among sampling years and springs with values for Alley and Blue springs of approximately 3 while those for Big, Pulltite, Round, and Welch springs were closer to 2. De ranged from 1.25 to 3.86 among sampling years and springs. Few non-native plant species occurred in the springs, and they accounted for <15% of the foliar cover across transects.

RESUMEN

Estudiamos las comunidades de vegetación acuática de siete grandes manantiales ubicados en Ozark National Scenic Riverways, Missouri, en 2007–2012. Este estudio proporciona una base para evaluar el impacto de las perturbaciones naturales y antropogénicas en la integridad ecológica de los manantiales. La vegetación se evaluó cuantitativamente a lo largo de cuadrantes de muestreo ubicados en varios transectos en cada manantial. Listamos 69 taxones diferentes con una considerable superposición de presencia de especies entre los manantiales, entre ellas 6 familias, 6 géneros, y 6 especies de algas, y 9 familias, 12 géneros, y 19 especies de musgos y hepáticas. Entre las angiospermas, registramos 10 familias, 13 géneros, y 20 especies de monocotiledóneas, y 16 familias, 23 géneros, y 24 especies de dicotiledóneas. Algunas especies previamente reportadas en los manantiales ya no están presentes, lo que puede deberse a cambios a largo plazo en la cuenca. Los cuadrantes de muestreo individuales típicamente contuvieron de cuatro a seis taxones, aunque Welch Spring en general sólo tuvo de dos o tres taxones representados. Los números efectivos de especies fueron generalmente consistentes entre años para todos los manantiales, pero las diferentes especies no tuvieron una abundancia igual en la comunidad en o entre años de muestreo. La riqueza de taxones fue ligeramente superior al número efectivo del Índice de Diversidad de Simpson (De) y al número efectivo del Índice de Diversidad de Shannon (He) para todos los años entre los manantiales. He varió de 1.34 a 3.76 entre los años de muestreo y los manantiales, con valores para los manantiales Alley y Blue de aproximadamente 3, mientras que los de los manantiales Big, Pulltite, Round, y Welch fueron cercanos a 2. De osciló entre de 1.25 a 3.86 entre años de muestreo y manantiales. Pocas especies de plantas no nativas estuvieron presentes en los manantiales, las cuales representaron < 15% de la cubierta foliar en los transectos.

Key Words: aquatic vegetation, floristics, community ecology, Ozarks, springs

INTRODUCTION

Mosses, algae, and higher plants are particularly important structural and biological constituents of springs and aquatic systems in general (Hannan & Dorris 1970; Cushing & Wolf 1984; Carpenter & Lodge 1986; Durarte & Canfield 1990; Stream Bryophyte Group 1999; Cantonati et al. 2006), and they often have complex

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relationships with some fish and aquatic invertebrates (Cyr & Downing 1988; Xie et al. 2005, 2006). Additionally, aquatic plants are important biological filters of a variety of chemical contaminants and nutrients (Demars & Harper 1998; Cantonati et al. 2006; Vardanyan & Ingok 2006). Aquatic vegetation communities in spring ecosystems are vulnerable to a broad variety of anthropogenic disturbances (Sanford 1979; Englund 1991; Schütz 1995; Preston et al. 2003). Land use, particularly vegetation clearing practices with associated increases in sediment and nutrient loads and other point and nonpoint inputs to surface water, has been reported as the greatest long-term threat to streams and springs in the Ozark Highlands (Duchrow 1977; Jacobson & Primm 1997; Scott & Udouj 1999; Imes & Frederick 2002). Recent studies of the possible effects of global climate change indicate that increases in annual average water temperature (Hogg & Williams 1996; Poff et al. 2002; Johnson 2007), changes in discharge (Erman & Erman 1995), and non-native (i.e., exotic) species introductions (Bowles & Bowles 2013) may impact spring communities as well. Therefore, aquatic vegetation surveys are important to researchers and managers to establish inventories and aid in the diagnosis of ecosystem disturbances. Monitoring changes in aquatic vegetation has long been used as an indicator of anthropogenic disturbance throughout Europe. This approach has received little attention in the United States (Romero & Onaindia 1995; Tremp & Kohler 1995; Small et al. 1996; Bartodziej & Ludlow 1997; Ali et al. 1999; Schorer et al. 2000; Bernez et al. 2001, Bernez 2004; Haury et al. 2002; Scott et al. 2002; Daniel et al. 2005; Haslam 2006). Documenting the occurrence and distributions of flora in springs provides a baseline for assessing the potential for, or extent of, a variety of both anthropogenic and natural disturbances and is an integral step toward their conservation and understanding their role in ecosystem function.

The extensive dolomitic karst topography in the area surrounding Ozark National Scenic Riverways (OZAR), Missouri, is conducive to the formation of springs (Mugel et al. 2009). Within the karst terrain of OZAR there are more than 425 springs. Although most of these springs are relatively small, several are defined as 1st and 2nd magnitude, having minimum discharges of 2.8 m^3/sec and 0.28 m^3/sec, respectively (Meinzer 1927). The largest (Big Spring) has a maximum recorded discharge greater than 36 m^3/sec and is ranked as one of the five largest springs in North America (Brune 1981). Springs at OZAR are highly vulnerable to biological and chemical degradation and may represent the ultimate challenge in water quality protection (Gibert 1990; Imes & Fredrick 2002). Despite the large amount of literature addressing groundwater contamination and its complexities, there is little information on the physical and biological impacts of contaminated groundwater within springs or within surface water fed by springs (Williams 1991; Notenboom et al. 1994; van der Kamp 1995).

Prior to this study, no long-term biomonitoring programs for aquatic vegetation were conducted for the springs at OZAR, although there had been some short-term studies of algae and aquatic vegetation completed. Drouet (1933) reported on the algae found in Big, Alley, and Round springs in addition to listing a few records for vascular plants. Steyermark (1941) conducted the first known inventory of aquatic plants in Missouri springs, including those assessed in this study, and he further corrected several misidentifications made by Drouet (1933). Lipscomb (1969) conducted a floristic inventory of the aquatic plants at eight springs at OZAR, and Currier (1990a, b) conducted floristic inventories at four springs. Redfearn et al. (without date) conducted a botanical survey of OZAR and listed some aquatic species although they did not focus on the springs. Redfearn (1981) addressed aquatic mosses and liverworts known to occur in Ozark springs, including those at OZAR. Converse (1994) conducted a quantitative study of hydrophyte production at Big Spring, but this work was never published. Most of these previous studies, described above, provided only qualitative data and no effort was made to quantify species densities.

To address this lack of knowledge of anthropogenic and natural disturbance effects on springs, we began a spring monitoring program in 2007 to provide a baseline for assessing the ecological integrity of springs at OZAR, including the aquatic vegetation community (Bowles et al. 2008). This paper includes a floristic inventory of the aquatic vegetation of OZAR springs and provides an analysis of plant community diversity dynamics, 2007–2012.

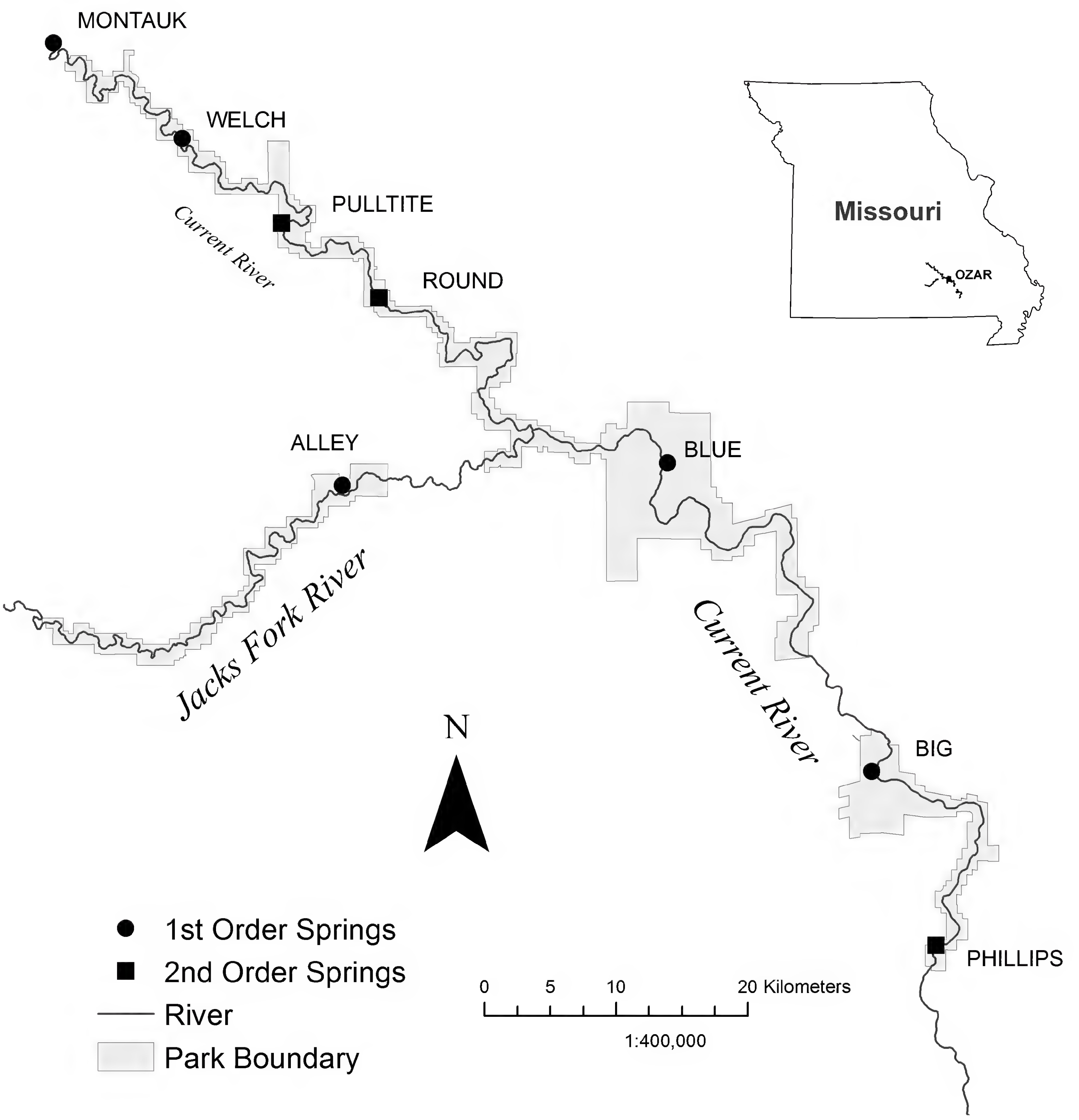
METHODS

Study sites.—Aquatic vegetation was assessed annually at each of six 1st or 2nd magnitude springs (Meinzer 1927; Vineyard et al. 1974) located at OZAR (Fig. 1), during late July–early August from 2007 to 2012. An additional 2nd order spring (Phillips Spring) was sampled in 2011 and 2012. Banks immediately adjacent to the spring branches generally are well-vegetated, undisturbed, and stable, although some of the springs have well-worn walking paths along at least one bank and/or managed lawns in their general vicinity. The riparian canopy for all the springs is generally less than 40%. Among springs, temperature ranged from 13.5 to 14.5 °C, dissolved oxygen concentration ranged from 8.2 to 11.1 mg/L, specific conductance ranged between 200 and 350 µS/cm, and pH fell between 7.2 and 7.6 at time of sampling. Turbidity was typically at low levels in the springs (<1 NTU) during sampling but was around 4 NTU at Big Spring in 2012 due to an apparent collapse within the spring conduit that caused the water to appear milky. Run habitat, defined here as deep, fast water with little or no turbulence, was dominant in all springs. Dominant substrate for all of the springs varied but generally consisted of large pebble to small cobble (32–90 mm). The substrate of Big and Round springs contained smaller mean substrate sizes, including a higher percentage of sands, compared to the other springs. Discharge among springs during sampling in 2007–2012 varied widely: Alley Spring (2.21–3.80 m^3/sec), Big Spring (9.85-13.93 m^3/sec), Blue Spring (2.19–3.97 m^3/sec), Pulltite Spring (0.37–2.21 m^3/sec), Round Spring (0.50–2.99 m^3/sec), Welch Spring (4.01–8.41 m^3/sec). Discharge for Phillips Spring was 0.58 m^3/sec in 2011 and 0.61 m^3/sec in 2012. A further assessment of the physical habitat is not included here.

Reach selection.—The portion of the spring run to be sampled was unique for each spring due to their respective sizes and other physical characteristics. One reach was sampled in each spring run and began as close to the spring source as practical, taking into consideration depth, flow, and crew safety near the spring source. Reach length was based on a weighting factor that accounted for variation among average widths to ensure a uniform sampling effort that represented each spring's total area, and facilitated inclusion of representative macrohabitats (Bowles et al. 2008). Reach lengths were Welch Spring (36 m), Phillips and Pulltite springs (150 m each), Blue Spring (160 m), Alley Spring (190 m), Round Spring (240 m), and Big Spring (540 m). The sampling reach was divided into 11 equally spaced transects perpendicular to flow with three sample cells (1 m^2) per transect. The only exception to this was Welch Spring, where only three transects were established because of the short spring run (36 m) from the source to the confluence with the Current River. Transects defined the sample locations with physical habitat sampled at each transect (N = 33; 9 Welch Spring) and aquatic vegetation sampled at odd numbered transects (six transects, N = 18; 9 Welch Spring) using a PVC sampling frame and view bucket to observe vegetation. The sampling frame was divided into quadrats to facilitate assessing vegetation abundance. Plant species foliar cover in each sample cell was recorded using a modified Daubenmire scale: 1 = 0–0.99%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95%, 7 = 95–100% (Daubenmire 1959; Bowles et al. 2008).

Data summary and analysis.—Data collected from all sample cells were summarized by taxa for the area sampled. Mean values along with a measure of variability (± 1 standard error of the mean) were calculated for the community. Foliar cover estimates for each species were used to determine measures of species diversity (McCune et al. 2002).

Foliar cover data were analyzed using the midpoints of the respective cover classes and were analyzed under two broad categories: 1) diversity and 2) individual species frequency. Diversity analyses included taxa richness, Shannon's Diversity Index (Shannon 1948), and Simpson's Diversity Index (Simpson 1949), which were subsequently expressed as effective number of species (S, He, De) (Hill 1973; Joust 2006; Bowles et al. 2008). Effective number of species for each diversity measure reflects the number of species found in a similar community when all species occur in equal density (Bowles et al. 2008). If all species occurred in equal abundance in the community within and among sample years, then taxa richness, Shannon's Diversity Index, and Simpson's Diversity Index would all be equal (Washington 1984). The advantage of converting Shannon's Diversity Index and Simpson's Diversity Index to effective number of species is that it makes their values linear thus allowing for direct comparison.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PHILLIPS
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Missouri
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■ 2nd Order Springs
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Fig. 1. Map showing the locations of large springs at Ozark National Scenic Riverways, Missouri. Montauk Springs was not included in this study.

Metrics calculated for individual species included individual species frequency, percent foliar cover, and species importance value (Bowles et al. 2008). Species importance values are a measure of the relative dominance of species in a spring community—the larger the importance value, the more important the species. We also calculated percent exotic taxa richness and the ratio of percent foliar cover of exotic species to percent foliar cover of all species. This latter metric serves as a measure of the relative dominance of non-native species and thus serves as means of assessing community disturbance.

Specimen processing and voucher specimens.—Most angiosperms were pressed and mounted on herbarium sheets following guidance issued by the University of Florida Herbarium (2015). Representative Lemnaceae were stored in 4% formalin. Bryophytes were air dried and stored in folded paper packets made from 100% cotton fiber paper. Identification keys used included Redfearn (1972), Godfrey and Wooten (1979, 1981), Flora of North America (1993+), and Yatskievych (1999, 2006, 2013). Voucher specimens are deposited in the National Park Service, Heartland Inventory & Monitoring Aquatic Program reference collection (HTLN) located at the

Department of Biology, Missouri State University, Springfield, Missouri. Other reference species are deposited in the Ozarks Regional Herbarium (SMS) located in the Department of Biology, Missouri State University, Springfield, Missouri. Common names follow USDA, NRCS (2014).

RESULTS

Floristic study.—A broad assemblage of aquatic vegetation occurs among the springs at OZAR with 69 distinct taxa reported from this study. A complete list of plant species recorded from transects in each spring is in the Appendix. We recorded 5 families, 5 genera, and 5 species of algae. We also found modest amounts of filamentous green algae (Chlorophyta) at all of our sites, but it was not identified to a more specific taxonomic level. We report 9 families, 13 genera, and 19 species of mosses and liverworts. Many of these were reported by Redfearn (1972) and were not identified by us. Among angiosperms, we list 10 families, 13 genera, and 20 species of monocots, and 16 families, 23 genera, and 24 species of dicots. Star duckweed (*Lemna trisulca*) was found at all springs except Pulltite and Welch springs. This species has a S2 state heritage ranking, indicating it is imperiled because of rarity or other factors, thus making it vulnerable to extirpation in Missouri. The environmentally sensitive red alga, *Batrachospermum,* occurs in all of the springs (Barinova 2013).

We found examples of *Elodea canadensis* and *Elodea nuttallii* in most of the springs. It was not practical to distinguish these two taxa in the vegetative state while doing the community assessment. Based on flowering specimens we found, it appears that *E. canadensis* is the more abundant of the two species. Additionally, Yatskievych (1999) noted that specimens intermediate between these two species are known to occur in the region, suggesting they may produce hybrids. Our observations support that notion, and we treat the two species at the generic level for the community analysis.

Two closely related species, *Veronica anagallis-aquatica* and *Veronica catenata*, occur within the range of the springs we sampled. These two species can be separated most easily on the basis of leaf size and shape. Yatskievych (2013) considers *V. anagallis-aquatica* to be non-native, whereas *V. catenata* is native. Although *V. catenata* commonly occurs as a submerged aquatic, Yatskievych (2013) noted that the vegetative plants of *V. anagallis-aquatica* also may occur as submerged aquatics and would be morphologically indistinguishable from those of *V. catenata*. Vegetative forms of *Veronica* occurred in all of the springs we sampled, but based on reproductive forms of *Veronica* we found, we have identified this species as *V. catenata*. It is possible that hybrids between these two species may exist (Yatskievych 2013). In contrast, USDA, NRCS (2014) treats these two species as synonyms with *V. catenata* being a junior synonym of *V. anagallis-aquatica*, and further considers this species to be native.

Few non-native (exotic) plants occurred in the springs. The most commonly occurring non-native plant was water-cress (*Nasturtium officinale*), but other introduced species included annual bluegrass (*Poa annua*), watermint (*Mentha aquatica*), creeping bentgrass (*Agrostis stolonifera*), creeping jenny (*Lysimachia nummularia*), and bitter dock (*Rumex obtusifolius*). It is possible that the species we identify as *M. aquatica* may be a hybrid of that species and *Mentha spicata* L. (=*M.* × *piperita* L.) as described by Yatskievych (2013), but we were unable to make that determination. Although all of these species are considered terrestrial or wetland plants, they grow in the spring runs at OZAR where some specimens are completely submersed. Invasive species, including *Myriophyllum spicatum* are present in the Current River basin (Padgett 2001, personal observations both authors) and may eventually enter the springs, especially in areas having slow current velocities.

Unusual findings include examples of fully submersed terrestrial or wetland species including *Lobelia cardinalis*, *Lysimachia nummularia*, *Mentha aquatica*, *Physostegia virginiana, Poa annua*, and *Rumex obtusifolius*. We have found examples of *R. obtusifolius* at Big Spring near mid-channel (~20 m from bank) in water approximately 1.5 m deep. *Physostegia virginiana* grows completely submersed at Blue Spring where plants are distributed over a 15 m patch located on the right side of the channel downstream of the spring source in water approximately 1 m deep. The present distribution of *P. virginiana* at Blue Spring is in the same general area as that reported by Steyermark (1941). We also found a small clump of *P. virginiana* growing submersed at Alley Spring, but that clump subsequently disappeared. At Phillips Spring, *L. cardinalis* produces inflorescences that extend above the surface of the water at mid-channel while the stems and leaves remain submersed. *Lysimachia nummularia* and *M. aquatica* are commonly encountered along the margins of the springs at OZAR and we commonly find submersed plants of both species. *Poa annua* can be found at many springs in the Ozarks region where it grows submersed.

Several species previously reported from some springs (Steyermark 1941; Currier 1990a, b) were not found during this study. These species and the springs from which they were formerly known include: three species of *Juncus* (Round, Welch); creeping bentgrass, *Agrostis stolonifera* (Blue); grassleaf mudplantain, *Heteranthera dubia* (Big, Blue); star duckweed, *Lemna trisulca* (Pulltite); horned pondweed, *Zannichellia palustris* (Big, Round, Welch; now only found at Blue where it is rare); Illinois pondweed, *Potamogeton illinoensis* (Alley, Big, and Welch); long beak buttercup, *Ranunculus aquatilis* (Alley, missing at Welch in 2008 and 2009); and leafy pondweed, *Potamogeton foliosus* (Alley, Big, Pulltite). The community data we present are based on transect data, but a thorough visual inspection of the areas between transects and areas above and below the sample reaches did not locate these species. Numerous other species of plants occurred in the springs at OZAR, but they were not present in sample cells (see Appendix).

Community diversity.—The highest richness among springs based on transect data from all years combined was at Round Spring, where 20 taxa were found, whereas Alley and Blue springs each had 19 taxa. Seventeen taxa were found across transects at Big Spring, whereas Pulltite, Welch, and Phillips had the fewest taxa (15, 13, and 11 taxa, respectively). Individual sample cells typically contained four to six taxa, although Welch Spring generally had only two to three species represented. In general, Welch Spring shared the fewest species in common with the other springs, which may be due to its short (36 m) spring run, smaller sample size (3 transects), and high current velocities that limit vegetation growth in the mid-channel. Because the Welch spring run is short, we were able to visually examine most of the entire bottom, and based on those observations, the low taxa richness estimates for that spring are accurate. Foliar coverage of aquatic vegetation was extensive in all of the springs, with bare substrate occupying 20% or less of sample cells on average. Effective numbers of species (S, He, and De) were generally consistent among years for all springs (Fig. 2 a–f), and the various species did not occur in equal abundance in the community within and among sample years. Taxa richness was higher than De and He for all years among springs, and the difference between those values was around two fold or less in most cases. The Mean Shannon's Index effective number (He) ranged from 1.34 to 3.76 among sampling years and springs, with values for Alley and Blue springs approximately 3 while those for Big, Pulltite, Round, and Welch springs were generally closer to 2. Simpson's Index effective numbers (De) ranged from 1.25 to 3.86 among sampling years and springs. Similar to the values recorded for He, De values were highest for Alley and Blue springs compared to the other springs. At Phillips Spring, taxa richness during 2011 and 2012 was 3.11 (±0.59) and 2.22 (±0.11); He was 2.22 (±0.32) and 1.73 (±0.02); and De was1.96 (±0.28) and 1.58 (±0.04).

Mosses and algae occurred most frequently and had the greatest percent foliar cover among all springs except for Big and Round springs (Figs. 3–4). *Nasturtium officinale* and *Cardamine bulbosa* had the highest Individual Species Frequency (ISF) and Percent Foliar Cover (PFC) at Alley Spring (Fig. 3a). At Big Spring, *Ranunculus aquatilis* had the highest ISF and PFC (Fig. 3b). *Lemna trisulca* was more frequently encountered compared to the other flowering species at Blue Spring, but the PFC for all angiosperms was relatively low (Fig. 3c). At Pulltite Spring, *Persicaria hydropiperoides* and *N. officinale* were the most common flowering plants (Fig. 3d), while several taxa were co-dominant at Round Spring (Fig. 4a). *Myriophyllum heterophyllum* and *N. officinale* were the most dominant angiosperms encountered at Welch Spring (Fig. 4b). Only six angiosperms were recorded on transects at Phillips Spring and all had relatively low PFC values (Fig. 4c). Mean Species Importance Values (SIV) among springs clearly showed that some taxa were more important than others, which is not always reflected by their ISF and PFC values when considered independently (Table 1). Collectively, mosses and algae had the highest SIVs at all springs. Among angiosperms, *N. officinale* and *C. bulbosa* had the highest SIVs at Alley Spring (SIV = 14.24 and 13.96, respectively). *Ranunculus aquatilis* was the most important species at Big Spring (SIV = 38.89) followed by *N. officinale* (SIV = 17.09). At Blue Spring, *C. bulbosa, L. trisulca*,

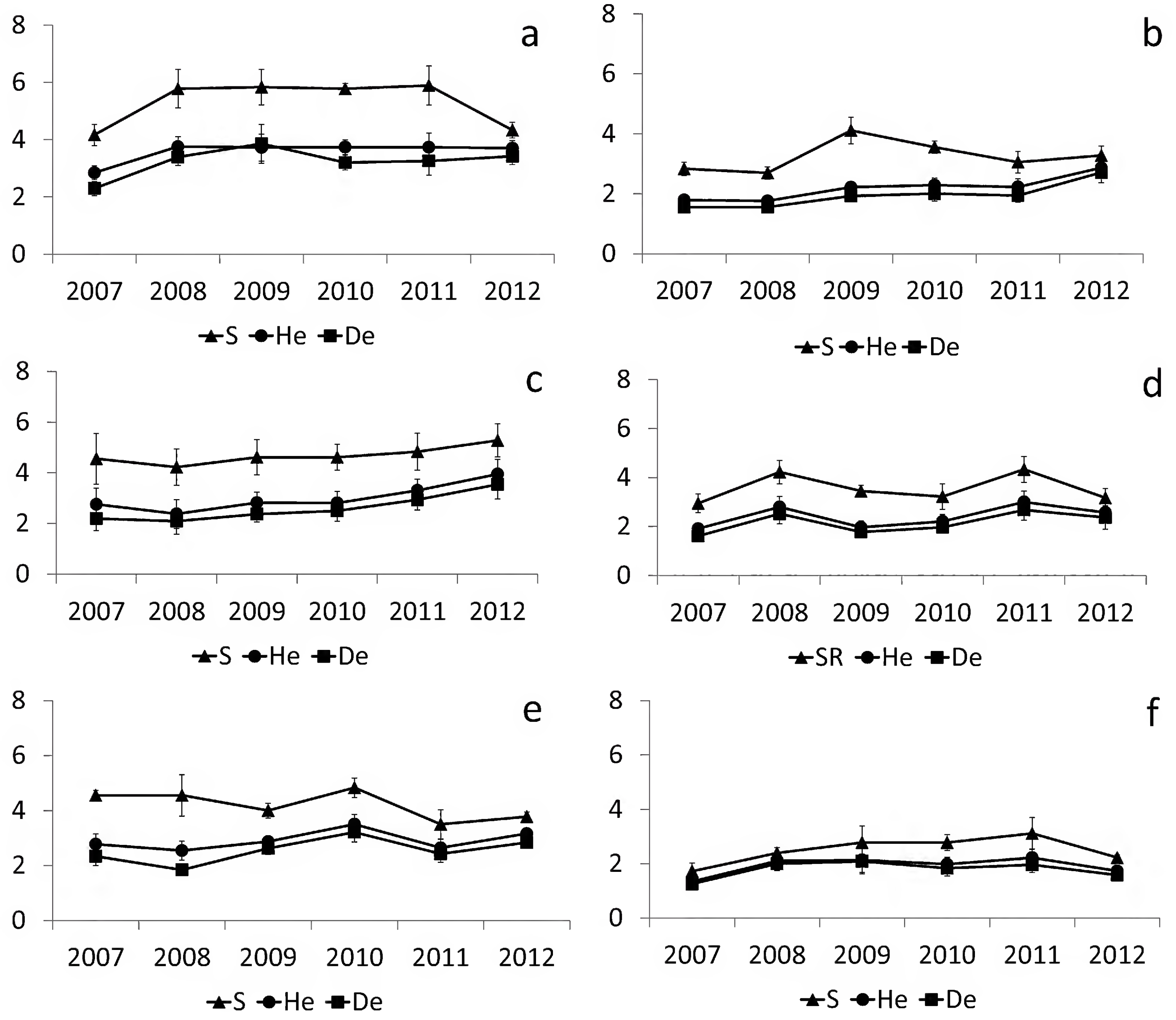

Fig. 2. Mean and standard error of effective numbers of species for aquatic vegetation occurring in six large springs at Ozark National Scenic Riverways, Missouri. S = taxa richness, He and De = effective number of species for Shannon's Diversity Index and Simpson's Diversity Index, respectively: (a) Alley Spring, (b) Big Spring, (c) Blue Spring, (d) Pulltite Spring, (e) Round Spring, (f) Welch Spring.

and *Veronica catenata* had the highest SIVs (9.13, 7.00, and 4.41, respectively). *Persicaria hydropiperoides* was the most important species at Pulltite Spring (SIV = 8.16) followed by *Elodea* spp. (SIV = 5.04). At Round Spring, *M. heterophyllum*, *Sparganium americanum* and *Potamogeton illinoensis* shared similar importance values (SIV = 16.33, 15.34, and 14.82, respectively). Welch Spring had *M. heterophyllum* and *N. officinale* as the most important species (SIV = 20.70 and 12.49, respectively), and *N. officinale* also had the highest SIV at Phillips Spring (SIV = 13.71).

Non-native species were poorly represented among all springs and their percent foliar cover was ≤15% across transects. The most commonly encountered and abundant non-native species was *Nasturtium officinale*, while *Mentha aquatica*, *Poa annua*, and *Rumex obtusifolius* were found less frequently. Non-native species generally had low SIVs, but *N. officinale* was the most important species at Alley and Phillips springs and among the most important species at Big, Welch, and Pulltite springs. Although *N. officinale* was commonly encountered in the spring runs, the majority of the foliar coverage for this species was near the wetted margins out of the main spring flows. The individual plants of *N. officinale* we encountered in the faster spring flows of the main channels typically had low percent foliar cover.

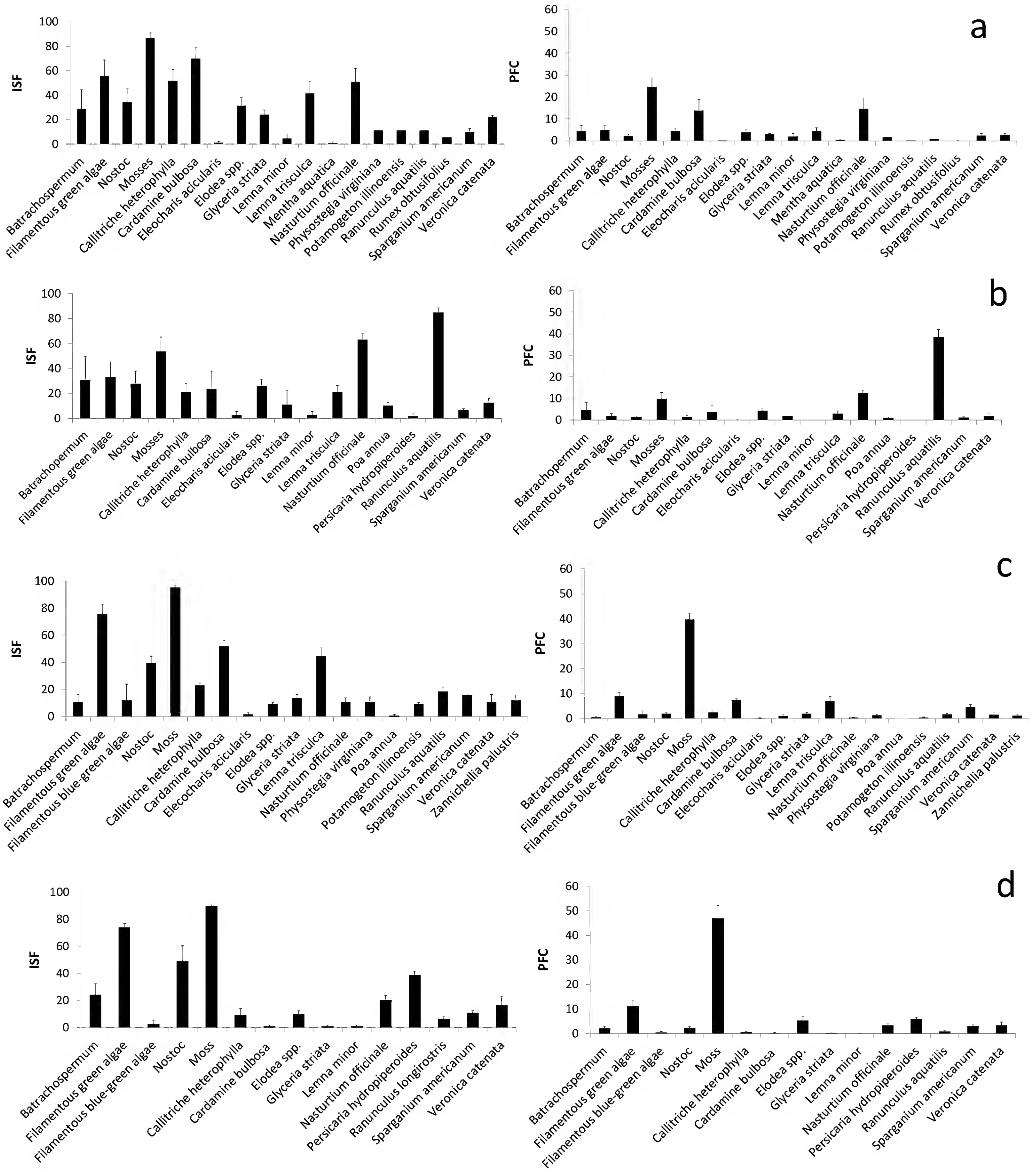

Fig. 3. Individual Species Frequency (ISF) and Percent Foliar Cover (PFC) for aquatic vegetation occurring in (a) Alley, (b) Big, (c) Blue, and (d) Pulltite springs at Ozark National Scenic Riverways, Missouri, 2007–2012.

DISCUSSION

Because of their unique and often independent sources, springs typically have a mosaic structure, a high degree of individuality, and typically an azonal character attributed to their physiochemical stability (Williams & Danks 1991; Cantonati et al. 2006). The monitoring results presented here generally support that assessment. The aquatic plant communities of the springs we studied are diverse and dynamic, and they share many species in common. In general, mosses and algae were the dominant taxa among most springs. The lack of

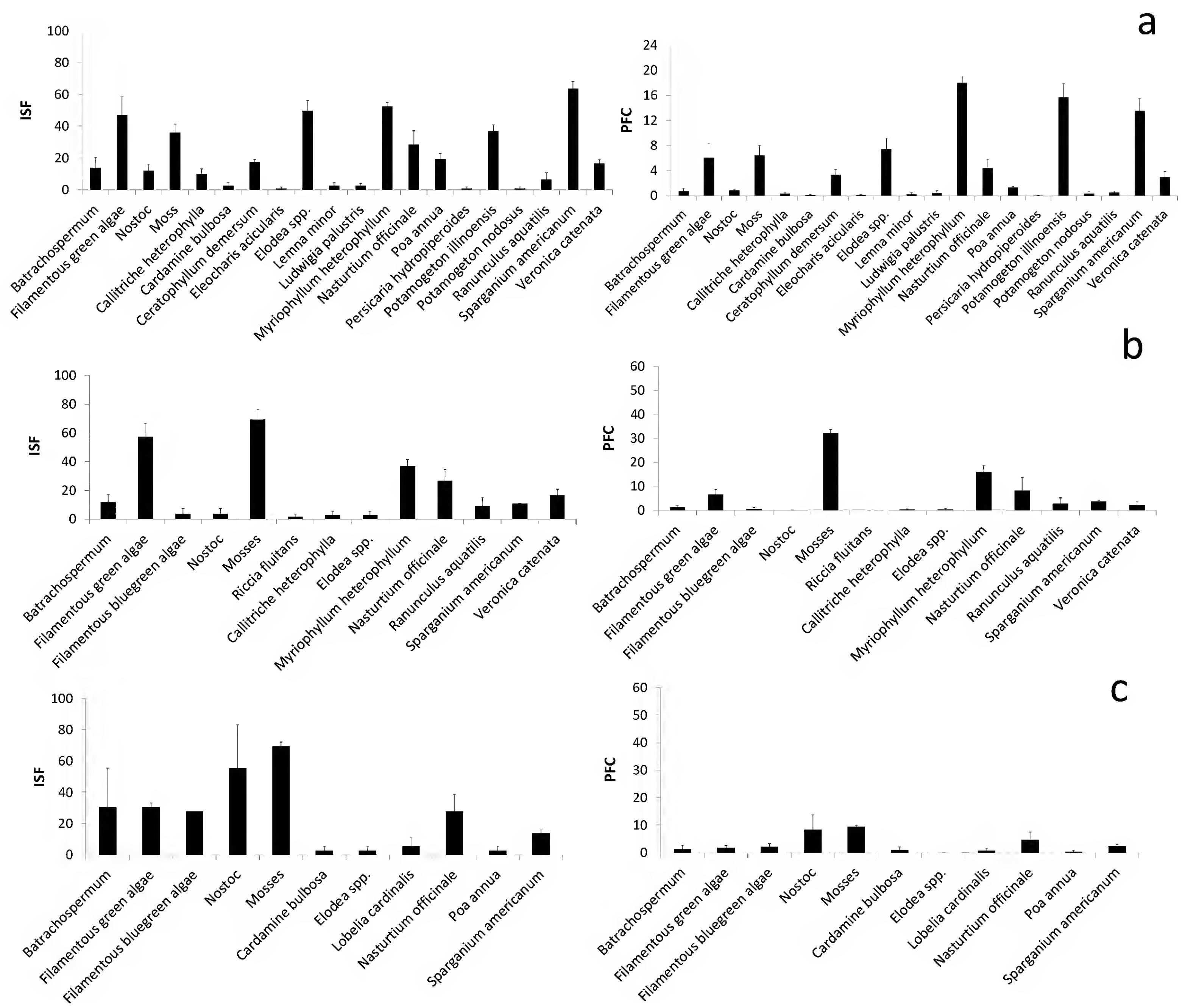

Fig. 4. Individual Species Frequency (ISF) and Percent Foliar Cover (PFC) for aquatic vegetation occurring in (a) Round, (b) Welch, and (c) Phillips springs at Ozark National Scenic Riverways, Missouri, 2007–2012.

dominance by mosses at Big and Round springs may be due to these systems having a predominance of sand substrates compared to gravel and cobble substrates found in the other springs.

The diversity of aquatic vegetation in the springs reported here was not unexpected. The findings of Steyermark (1941), Lipscomb (1969), and Currier (1990a, b) suggest aquatic plant community structure in these springs is dynamic. Currier (1990a, b) reported that the plant community structure in several springs had changed since Steyermark's study (Steyermark 1941), with some species apparently disappearing and others documented for the first time. For example, Steyermark (1941) reported horned pondweed (*Zannichellia palustris*), leafy pondweed (*Potamogeton foliosus*), and submerged stands of the non-native annual bluegrass (*Poa annua*) at Big Spring, but Currier (1990b) did not find those species. In contrast, Lipscomb (1969) found these three species were present at Big Spring. Our study found *P. annua* in Big Spring, but no representatives of leafy pondweed were detected. Steyermark (1941) did not record star duckweed (*Lemna trisulca*) or longbeak buttercup (*Ranunculus aquatilis*) from Big Spring, but these species are now present and abundant there (Lipscomb 1969; Currier 1990b; this study). Our data show that some species, such as swamp smartweed (*Persicaria hydropiperoides*) at Pulltite Spring, have made substantial increases in their foliar coverage since monitoring was initiated while others have decreased. Steyermark (1941) reported *Heteranthera dubia* from the lower portion of Blue Spring, whereas Lipscomb (1969) reported this species from near the confluence of the spring with the

Table 1. Mean species importance values for aquatic vegetation at large springs located at Ozark National Scenic Riverways, Missouri.

	Alley	Big	Blue	Pulltite	Round	Welch	Phillips
Batrachospermum spp.	7.18	6.87	1.60	4.06	2.17	4.70	8.83
Filamentous green algae	8.68	6.50	14.50	16.41	8.77	17.03	7.15
Filamentous blue-green algae	—	—	2.19	0.51	—	3.89	9.03
Nostoc sp.	5.34	4.13	5.50	7.24	1.82	1.81	21.93
Mosses	24.44	14.02	34.02	40.68	7.94	42.01	27.68
Riccia fluitans	—	—	—	—	—	0.28	—
Callitriche heterophylla	7.59	3.49	2.89	1.44	1.14	1.12	—
Cardamine bulbosa	13.96	4.88	9.13	0.30	0.70	—	2.96
Ceratophyllum demersum	—	—	—	—	4.55	—	—
Eleocharis acicularis	0.76	0.76	0.20	—	0.15	—	—
Elodea spp.	5.15	6.62	1.06	5.04	10.24	0.58	0.36
Glyceria striata	4.19	2.58	3.04	0.18	—	—	—
Lemna minor	2.55	1.23	—	0.12	0.46	—	—
Lemna trisculca	6.58	4.53	7.00	—	—	—	—
Lobelia cardinalis	—	—	—	—	—	—	1.83
Ludwigia palustris	—	—	—	—	0.61	—	—
Myriophyllum heterophyllum	—	—	—	—	16.33	20.70	—
Mentha aquatica	0.50	—	—	—			—
Nasturtium officinale	14.24	17.09	1.71	4.12	5.69	12.49	13.78
Physostegia virginiana	2.20	—	1.65	—	—	—	—
Poa annua	—	2.72	0.20	—	3.04	—	0.74
Persicaria hydropiperoides	—	0.45	—	8.16	0.15	—	—
Potamogeton illinoensis	0.97	—	0.85	—	14.82	—	—
Potamogeton nodosus	—	—	—	—	0.35	—	—
Ranunculus aquatilis	0.30	38.89	2.48	1.58	1.06	3.01	—
Rumex obtusifolius	0.59	—	—	—	—	—	—
Sparganium americanum	2.40	1.81	3.00	4.26	15.34	4.91	5.71
Veronica catenata	3.99	3.02	4.41	3.77	3.56	3.78	—
Zannichellia palustris	—	—	0.23	—	—	—	—

Current River. In contrast, Currier (1990a) did not report *H. dubia* from Blue Spring, and we only found a few examples below its confluence with the Current River. The extant conditions of the watersheds of the springs have changed appreciably since Steyermark began his floristic study of Ozark springs in 1928 (Steyermark 1941). The historic Ozark forest was largely deforested by the late 1920s resulting in heavy gravel and silt loads entering waterways (Benac & Flader 2004), in addition to lessening recharge times into the source aquifer. Such impacts could have altered their vegetation communities at the time Steyermark studied them. Forest cover has now largely recovered, but it remains unclear how close the extant vegetation communities of the springs are to their historic conditions. It is possible that "weedy" species such as *P. foliosus* and *H. dubia* may no longer occur in the springs because those habitats have become more stable as the landscape has recovered. Conversely, species such as *L. trisulca* and *R. aquatilis* now find those habitats favorable.

The data presented here reflect the broad natural habitat diversity, and physical and chemical stability in these springs. Geographic location of the springs does not appear to be a primary contributing factor in the composition of their respective vegetation communities. Rather, watershed-level characteristics (recharge zone), local physical habitat factors including substrate size, canopy cover, and other unknown contributing factors may play important yet undetermined roles in structuring these communities. However, collecting and analyzing additional monitoring data is required to determine the importance and relative contribution of these environmental factors. Additional monitoring also will allow insight into any patterns that may exist in plant community structure among these springs. Furthermore, our data will be useful in gaging impacts to the springs from anthropogenic disturbances, potentially ensuring their protection.

APPENDIX

Springs: 1=Alley Spring, **2**=Big Spring, **3**=Blue Spring, **4**=Phillips Spring, **5**=Pulltite Spring, **6**=Round Spring, **7**=Welch Spring.
Growth Habit Types: Emergent=**E**, Floating=**F**, Submersed=**S**, Wetted margin=**W**
Non-native species are designated by an asterisk (*)
Collector/Identifier: D.E. Bowles, unless noted otherwise.
Collection number: (HTLN#)

ALGAE (5 families, 5 genera)

Batrachospermaceae
Batrachospermum spp.: 1, 2, 3, 4, 5, 6, 7. S (HTLN 072)
Characeae
Nitella acuminata A. Braun ex Wallman: 2, 3. S (HTLN 083)
Nostocaceae
Nostoc sp.: 1, 2, 3, 4, 5, 6, 7 (HTLN 078). S
Oscillatoriaceae
Lyngbya sp.: 3, 4, 5 (HTLN 081). S
Xanthophyceae
Vaucheria sp.: 1, 3, 5, 6 (HTLN 080). S
Chlorophyta
unidentified filamentous green algae : 1, 2, 3, 4, 5, 6, 7 (HTLN 079).

MOSSES, LIVERWORTS (9 families, 13 genera)

Amblystegiaceae
Hygroamblystegium fluviatile (Hedw.) Loeske (streamside hygroamblystegium moss): 2, 5, 6, 7 (Redfearn 1972, 1981).
Hygroamblystegium noterophilum (Sull. & Lesq.) Warnst. (hygroamblystegium moss): 3 (Redfearn 1972, 1981).
Hygroamblystegium tenax (Hedw.) Jenn. (hygroamblystegium moss): 1, 2, 3 (Redfearn 1972, 1981).
Leptodictyum riparium (Hedw.) Warnst. (streamside leptodictyum moss): 1, 3, 5, 6, 7 (Redfearn 1972, 1981).
Brachytheciaceae
Brachythecium rivulare Schimp. (brachythecium moss): 1, 2, 3, 5, 6, 7 (Redfearn 1972, 1981).
Platyhypnidium riparoides (Hedw.) Dix. (platyhypnidium moss): 2 (Redfearn 1972, 1981).
Fontinalaceae
Fissidens bryoides Hedw. (bryoid fissidens moss): 1, 2, 3 (Redfearn 1972, 1981).
Fissidens fontanus (Bach. Pyl.) Steud. (fissidens moss): 1, 2, 3 (Redfearn 1972, 1981).
Fissidens filiformis Sull. & Lesq. (fontinalis moss): 3 (Redfearn 1972, 1981).
Fissidens grandifrons Brid. (largeleaf fissidens moss): 1, 2, 3, 5, 6 (Redfearn 1972, 1981).
Fontinalis hypnoides Hartm. var. *duriaei* (Schimp.) Husn. (fontinalis moss): 1, 2, 3, 5, 6, 7 (Redfearn 1972, 1981).
Fontinalis missourica Cardot (Missouri fontinalis moss): 3 (Redfearn 1972, 1981).
Pottiaceae
Hyophila involuta (Hook.) A. Jaeger (hyophila moss): 1, 2, 5, 7 (Redfearn 1972, 1981).
Thuidiaceae
Cyrto-hypnum pygmaeum (Schimp.) W.R. Buck & H.A. Crum (pygmy cyrto-hypnum moss): 2, 5 (Redfearn 1972, 1981).
Conocephalaceae
Conocephalum conicum (L.) Dumort. (liverwort): 2, 3, 4, 5, 6 (HTLN 085).
Marchantiaceae
Dumortiera hirsuta (Sw.) Nees (liverwort): 2, 3, 5 (Redfearn 1981, Timme & Redfearn 2011).
Marchantia polymorpha L. (liverwort): 1, 2, 3, 6, 7 (HTLN 084).
Porellaceae
Porella pinnata L. (liverwort): 1, 2, 3, 4, 7 (Redfearn 1981, Timme & Redfearn 2011) (HTLN 086).
Ricciaceae
Riccia fluitans L. (liverwort): 4, 7 (HTLN 073). F, S

VASCULAR PLANTS

MONOCOTS (10 families, 13 genera)
Alismataceae
Alisma subcordatum Raf. (American water plantain): 2 (HTLN 063). E
Sagittaria latifolia Willd. (broadleaf arrowhead): 2, 4, 6 (HTLN 004). E
Cyperaceae
Eleocharis acicularis (L.) Roem. & Schult (needle spikerush): 2, 3, 4, 5, 6 (HTLN 011). E, S
Hydrocharitaceae
Elodea canadensis Michx. (Canadian waterweed): 1, 2, 3, 4, 5, 6, 7 (HTLN 015). S
Elodea nuttallii (Planch.) H. St. John (western waterweed): 1, 2, 3, 4, 5, 6, 7 (HTLN 014, 089). S
Juncaceae
Juncus acuminatus Michx. (tapertip rush): 6, 7 (Steyermark 1941). E
Juncus dudleyi Wiegand (Dudley's Rush): 7 (Steyermark 1941). E
Juncus tenuis Willd. (poverty rush): 7 (Steyermark 1941). E
Lemnaceae
Lemna minor L. (common duckweed): 1, 2, 3, 5, 6 (HTLN 069). F
Lemna minuta Kunth (least duckweed): 6 (HTLN 076). F, S
Lemna trisulca L. (star duckweed): 1, 2, 3, 5 (HTLN 077). S
Poaceae
Agrostis stolonifera L. (creeping bentgrass)*: 3 (Steyermark 1941). E, W
Glyceria striata (Lam.) Hitchc. (fowl manna grass): 1, 3, 4, 6 (HTLN 027). E, S, W
Poa annua L. (annual blue grass)*: 1, 2, 4, 6, 7 (HTLN 028). E, S, W
Pontederiaceae
Heteranthera dubia (Jacq.) MacMill. (grassleaf mudplantain): 2, 3 (Steyermark 1941; HTLN 033). S
Potamogetonaceae
Potamogeton foliosus Raf. (leafy pondweed): 1, 2, 5, 6 (HTLN 034). S
Potamogeton illinoensis Morong (Illinois pondweed): 1, 2, 3, 4, 6, 7 (HTLN 036). S
Potamogeton nodosus Poir. (longleaf pondweed): 6 (HTLN 095). S
Sparganiaceae
Sparganium americanum Nutt. (American bur-reed): 1, 2, 3, 4, 5, 6 (HTLN 041). E, S
Zannichelliaceae
Zannichellia palustris L. (horned pondweed): 2, 3, 6, 7 (HTLN 082). S

DICOTS (16 families, 23 genera)

Acanthaceae

Justicia americana (L.) Vahl (American water-willow): 6 (HTLN 087). E, S

Balsaminaceae

Impatiens capensis Meerb. (jewelweed): 1, 2, 3, 4, 5, 6, 7 (HTLN 008). W

Brassicaceae

Cardamine bulbosa (Schreb. ex Muhl.) Britton, Sterns & Poggenb. (bulbous bittercress): 1, 2, 3, 4, 5, 6, (HTLN 006). S

Nasturtium officinale W.T. Aiton (watercress)*: 1, 2, 3, 4, 5, 6, 7 (HTLN 007). E, F, S, W

Callitrichaceae

Callitriche heterophylla Pursh (twoheaded water-starwort): 1, 2, 3, 5, 6, 7 (HTLN 009). S

Campanulaceae

Lobelia cardinalis L. (cardinalflower): 4 (HTLN 060). E, S, W

Ceratophyllaceae

Ceratophyllum demersum L. (coon's tail): 1, 2, 6 (HTLN 010). S

Crassulaceae

Penthorum sedoides L. (ditch stonecrop): 3 (HTLN 062). W

Haloragaceae

Myriophyllum heterophyllum Michx. (twoleaf water milfoil): 1, 2, 5, 6, 7 (HTLN 012). S

Myriophyllum spicatum L. (Eurasian watermilfoil)*: 1 (backwater only), (HTLN 052). S

Lamiaceae

Lycopus rubellus Moench (taperleaf water horehound): 3 (HTLN 047). E, W

Mentha aquatica L. (watermint): 1, 3, 4, 6, 7 (HTLN 017)*. E, S, W

Physostegia virginiana (L.) Benth. (obedient plant): 3 (HTLN 065). E, S, W

Onagraceae

Ludwigia palustris (L.) Elliott (marsh seedbox): 2, 4, 6 (HTLN 021). E, S, W

Polygonaceae

Persicaria hydropiperoides (Michx.) Small (swamp smartweed): 2, 4, 5, 6 (HTLN 045). E, S, W

Rumex obtusifolius L. (bitter dock)*: 1, 2, 3, 4, 5, 6, 7 (HTLN 032). E, S, W

Primulaceae

Lysimachia nummularia L. (creeping jenny)*: 2, 6 (HTLN 037). S, W

Samolus valerandi L. ssp. *parviflorius* (Raf.) Hultén (seaside brookweed): 4, 6 (HTLN 092). W

Ranunculaceae

Ranunculus aquatilis L. (longbeak buttercup, whitewater crowfoot): 1, 2, 3, 5, 7 (HTLN 037). S, W

Saururaceae

Saururus cernuus L. (lizard's tail): 2, 4 (HTLN 039). W

Scrophulariaceae

Lindernia dubia (L.) Pennell (false pimpernel): 7 (Steyermark 1941). W

Veronica catenata Pennell (water speedwell): 1, 2, 3, 5, 6, 7 (HTLN 025). E, S, W

Urticaceae

Pilea pumila (L.) A. Gray (Canadian clearweed): 1, 3, 4, 6 (HTLN 043). W

Boehemeria cylindrica (L.) Sw. (smallspike false nettle): 1, 2, 3, 4, 5, 6, 7 (HTLN 088). W

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CYPERUS GRANITOPHILUS (CYPERACEAE), A GRANITE OUTCROP ENDEMIC, NEW FOR TEXAS AND OKLAHOMA (U.S.A.)

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ABSTRACT

Cyperus granitophilus McVaugh (Cyperaceae) has been discovered at Enchanted Rock State Natural Area in Gillespie and Llano counties in the Llano Uplift of Central Texas. Examination of herbarium specimens of the closely related *C. squarrosus* L. revealed 18 additional collections (total of 27) of *C. granitophilus* from the Llano Uplift of Texas, 10 collections from the Wichita Mountains in Comanche and Greer counties, Oklahoma, and one collection from the Arbuckle Uplift in Johnston County, Oklahoma. All collections were from regions with granitic outcrops. These collections represent the first documented occurrences of *C. granitophilus* in Texas and Oklahoma and are disjunct approximately 1270 km from the nearest previously documented populations in the Piedmont of Alabama.

RESUMEN

Cyperus granitophilus McVaugh (Cyperaceae) ha sido descubierto en la Enchanted Rock State Natural Area en los condados Gillespie y Llano en el Llano Uplift de Texas Central. El examen de especímenes de herbario del muy relacionado *C. squarrosus* L. reveló 18 colecciones adicionales (total de 27) de *C. granitophilus* del Llano Uplift de Texas, 10 colecciones de las montañas Wichita en los condados Comanche y Greer, Oklahoma, y una colección del Arbuckle Uplift en el condado de Johnston, Oklahoma. Todas las colecciones proceden de regiones con afloramientos graníticos. Estas colecciones representan las primera ocurrencias documentadas de *C. granitophilus* en Texas y Oklahoma y tienen una disyunción de unos 1270 km desde las poblaciones documentadas más próximas en el Piedmont de Alabama.

INTRODUCTION

Cyperus granitophilus McVaugh was first described by Rogers McVaugh in 1937 from a granite outcrop in Georgia (McVaugh 1937). This granite outcrop endemic is primarily restricted to the Piedmont region of the southeastern United States (Ware et al. 2011) with records from Georgia (McVaugh 1937), South Carolina (Hill & Horn 1997), Alabama, North Carolina, Tennessee, and Virginia (Estill & Cruzan 2001) (Fig. 1). *Cyperus granitophilus* is typically found in the dry, shallow soil zone bordering exposed granite bedrock and is often dominant in these areas (Ware et al. 2011). Burbanck and Platt (1964) refer to this zone as the "lichen-annual herb" community with a maximum soil depth of 7 to 15 cm. The species is also found in "scattered tufts" in the shallow soil areas of their "annual-perennial herb" communities which typically have deeper soils, up to 39 cm.

Cyperus granitophilus is often found growing in association with the closely related species *C. squarrosus* L. (Murdy 1968). McVaugh (1937) distinguished *C. granitophilus* from *C. squarrosus* by its slightly longer and wider spikelets, longer scales, 4 vs 3 lateral nerves on the scale, and non-stipitate achene (Fig. 2). McVaugh (1937) indicates that *C. granitophilus* can also be distinguished by its "somewhat stiffer culms, its densely crowded capitate inflorescence and somewhat coarser appearance, and by the awns of its spikelet-scales, which are spreading instead of reflexed as they often are in *C. inflexus* (*C. squarrosus*)." McVaugh indicates that while there is some overlap in the size measurements of the two species there is no intergradation in the achene character. *Cyperus granitophilus* is documented as an autotetraploid derivative of *C. squarrosus* (Garoni & Murdy 1964; Wynne 1964) with consistently higher chromosome numbers in *C. granitophilus* ($2n$ = ca. 80, 88, 96) versus *C. squarrosus* ($2n$ = ca. 48, 56, 64) (Murdy 1968).

METHODS AND RESULTS

During a study of the flora of Enchanted Rock State Natural Area, Llano and Gillespie counties, Texas, during the summer of 2014, *Cyperus granitophilus* was discovered at six locations, one in Gillespie County and five in

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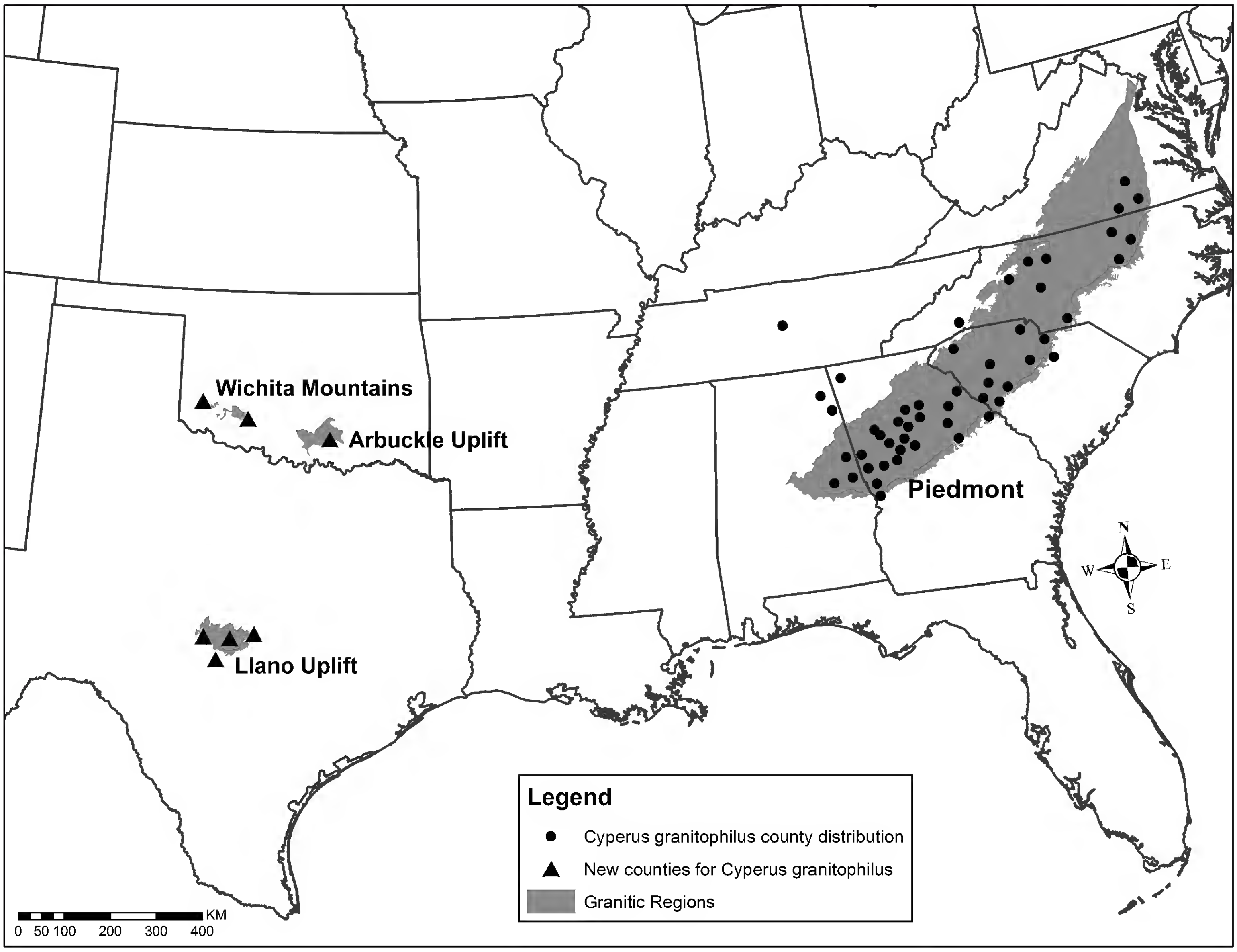

Fig. 1. Map showing updated county level distribution for *C. granitophilus* in the Eastern United States (Kartesz 2014; US Environmental Protection Agency 2013).

Llano County. The five main population centers within the park include 1) vernal pools on the summit of Enchanted Rock, 2) vernal pools on Little Rock, 3) seasonal seepage areas over granite rock west of Little Rock, 4) granitic sand over granite bedrock on Sandy Creek, and 5) a granite dike approximately 30 cm wide intruding in an area of Packsaddle Schist. This last population consisted of very few plants and is surrounded by habitat that is not suitable for the species.

Plants at Enchanted Rock State Natural Area were found growing in shallow soil no more than 15 cm in depth, but typically less than 5 cm. These shallow soil zones were found on the edges of exposed granite on the margins of vernal pools, cracks in granite, and granitic sand along drainage ways (Fig. 3). The plant was typically found in areas with slightly increased moisture relative to surrounding areas. Associated species include *Bulbostylis capillaris* (L.) Kunth ex C.B. Clarke, *Calibrachoa parviflora* (Jussieu) D'Arcy, *Cyperus haspan* L., *C. squarrosus*, *Elatine brachysperma* A. Gray, *Hypericum drummondii* (Grev. & Hook.) Torr. & A. Gray, *Hypericum gentianoides* (L.) B.S.P., *Ipomoea costellata* var. *edwardsensis* R. O'Kennon & Nesom, *Isoëtes lithophila* N.E. Pfeiffer, *Lepuropetalon spathulatum* Ell., *Lindernia dubia* var. *anagallidea* (Michx.) Cooperrider, *Phemeranthus parviflorus* (Nutt.) Kiger, *Portulaca pilosa* L., *Sedum nuttallii* Torr. & James ex Eat., *Selaginella corallina* (Riddell) Wilbur & Whitson, *Steinchisma hians* (Ell.) Nash, *Tripogon spicatus* (Nees) Ekman, and *Utricularia cornuta* Michx.

The authors conducted a thorough examination of specimens of the closely related species *Cyperus squarrosus* (= *C. aristatus*, *C. inflexus*) from the following herbaria: BRIT, OKL, SMU, TAMU, TEX-LL, VDB. During this process, 18 additional specimens of *C. granitophilus* (total of 27) were discovered in four Texas counties:

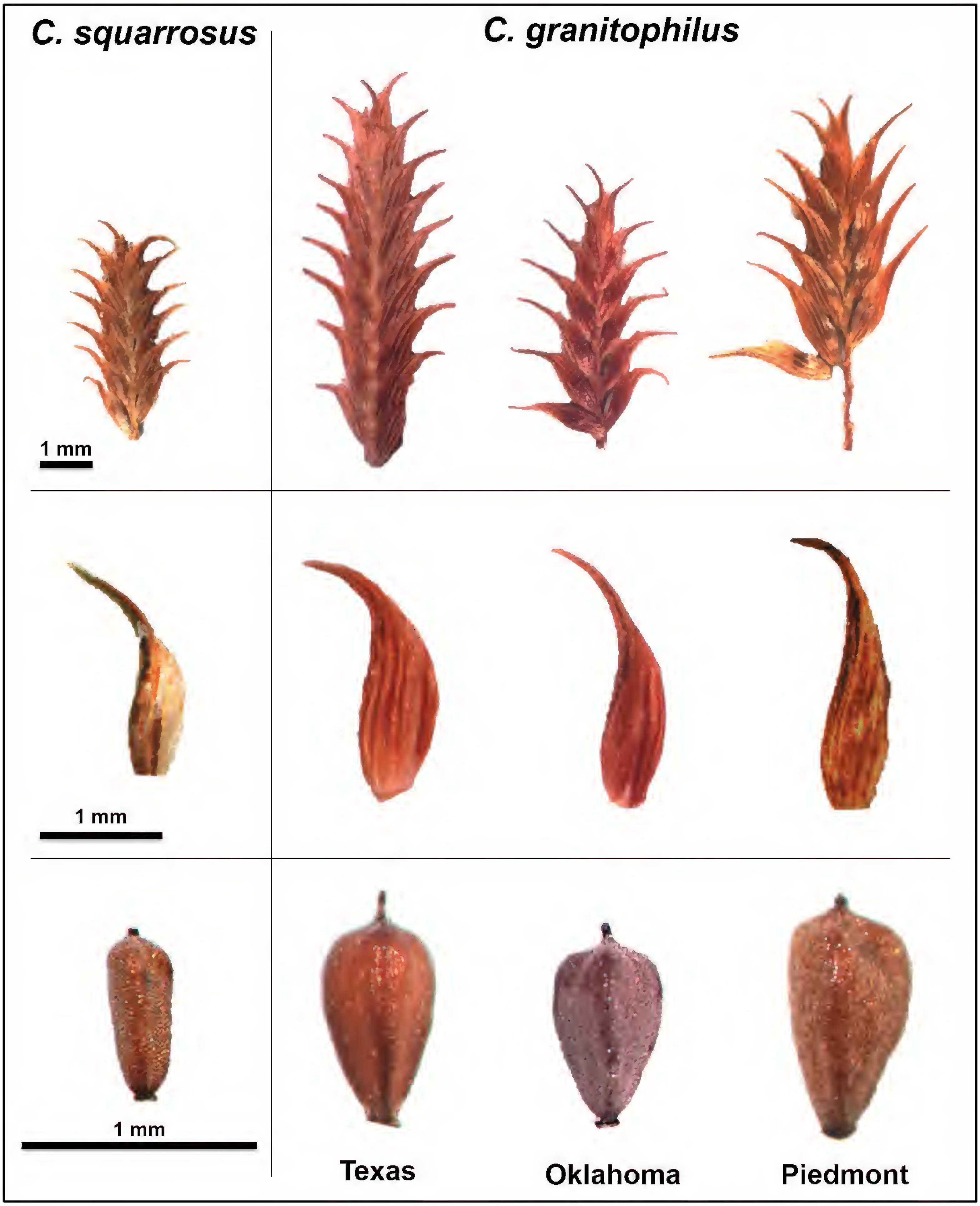
C. squarrosus
C. granitophilus
1 mm
1 mm
1 mm
Texas
Oklahoma
Piedmont

Fig. 2. Spikelets (top), floral scales (middle), and achenes (bottom) of *C. squarrosus* (*O'Kennon 8128a*, BRIT), and *C. granitophilus* from the Llano Uplift of Texas (*O'Kennon, Taylor & Rehman 26142*, BRIT), the Wichita Mountains of Oklahoma (*Waterfall 2904*, OKL), and the Piedmont Granite of South Carolina (*Hill 20023*, BRIT).

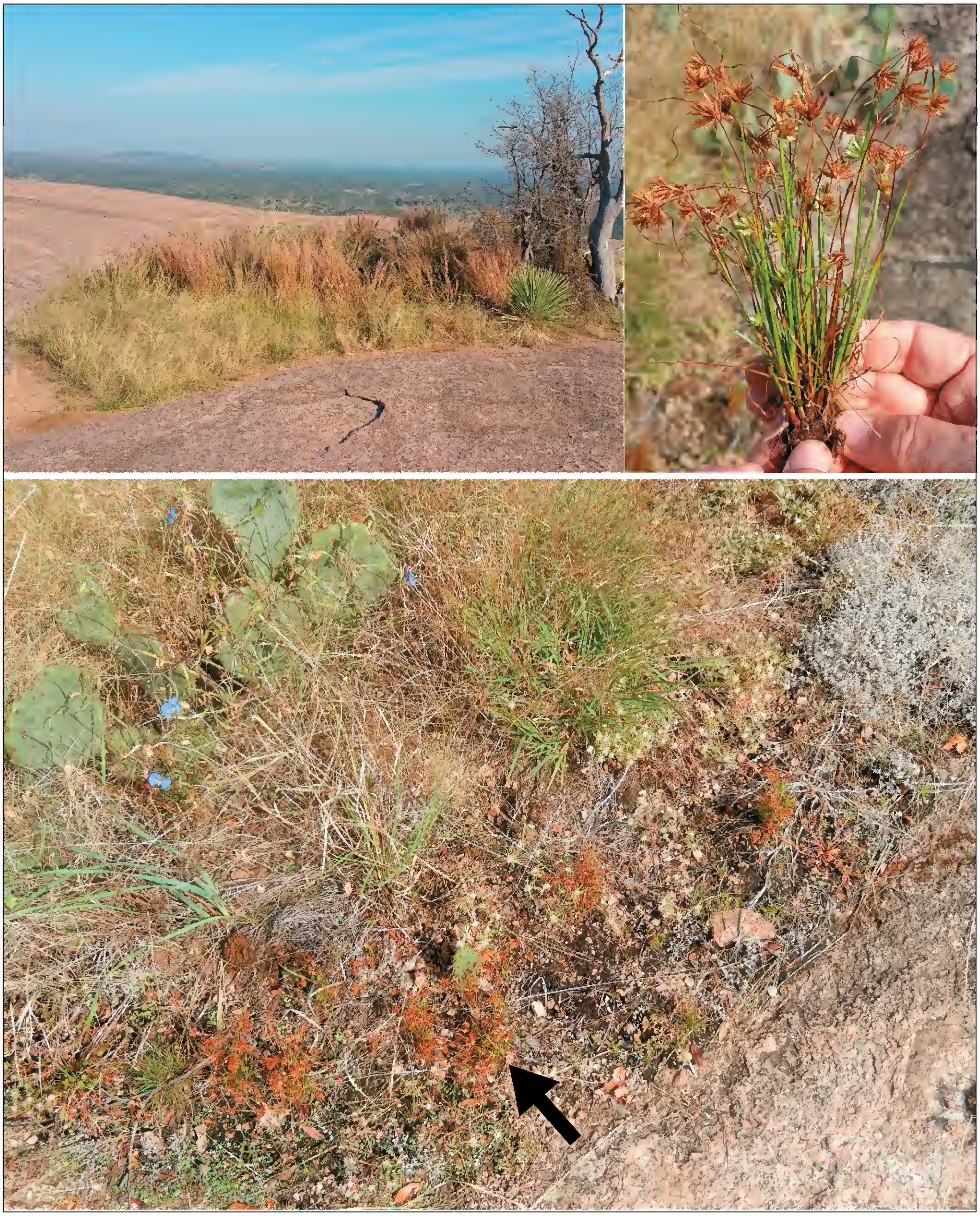

Fig. 3. Images of *C. granitophilus* and its habitat at Enchanted Rock State Natural Area. Top left: vernal pool on summit of Enchanted Rock; top right: image of plant; bottom: *C. granitophilus* growing in shallow soil near edge of granite rock.

Burnet, Gillespie, Llano, and Mason; and 11 specimens in three Oklahoma counties: Comanche, Greer, and Johnston. All of the Texas collections are from the Llano Uplift while all of the Oklahoma specimens are from the Wichita Mountains or Arbuckle Uplift (Fig. 1). These new populations in Texas and Oklahoma are disjunct approximately 1270 km (790 mi) from the western most location in Alabama.

Since *Cyperus granitophilus* does not occur in any regional floras within Texas or Oklahoma it is not surprising that specimens from the region were misidentified as *C. squarrosus*. *Cyperus granitophilus* is widely distributed across the Llano Uplift and observations at Enchanted Rock State Natural Area suggest it is likely a common member of the granitic flora in the region. Additional exploration of granite outcrops in both Texas and Oklahoma will undoubtedly reveal additional populations.

DISCUSSION

The Llano Uplift of central Texas, and the Wichita Mountains and Arbuckle Uplift of Oklahoma are all regions with large expanses of exposed granite, similar to that in the Piedmont of the southeastern United States where *Cyperus granitophilus* is wide-spread. The Llano Uplift of Texas spans 10 counties and includes approximately 5180 km^2 on the eastern margin of the Edwards Plateau (Walters & Wyatt 1982). It is composed of Precambrian granites, gneisses, and schists surrounded by escarpments of Paleozoic and Mesozoic limestone and sandstone. The region was once covered by Cretaceous limestone and sandstone with the granite basement rock being exposed due to erosion during the Miocene and Pliocene (Walters & Wyatt 1982). Therefore the Llano Uplift is a "topographical basin consisting of exposed Precambrian metamorphic rocks and large massifs of Precambrian granite surrounded by a discontinuous rim of Cretaceous limestone" (Walters & Wyatt 1982).

The Wichita Mountains of Oklahoma are primarily in Comanche County, but enter four additional counties, covering approximately 945 km^2 (US Environmental Protection Agency 2013). These rugged hills of igneous granite, granite-porphyry, diabase (dolerite), and gabbro rise above a relatively flat plain of Cambrian and Ordovician sandstone and limestone (Taff 1928).

The Arbuckle Uplift of Oklahoma, including the Arbuckle Mountains, is a plateau moderately elevated above the surrounding plain entering seven counties and covering approximately 3066 km^2 (US Environmental Protection Agency 2013). The area is predominately Cambrian to Devonian limestone with Carboniferous shales, sandstones, and conglomerates on the borders. A mass of granite, granite-porphyry, diabase, and associated crystalline rocks can be found in the central part of the uplift. Igneous rocks are exposed in three areas, with the largest in the east composed mostly of granite and diabase dikes. The surface granite is nearly flat and much of it is concealed by materials produced by its own disintegration (Taff 1928).

The granites of the Wichita Mountains, Arbuckle Uplift, and Llano Uplift are markedly similar in structure (Taff 1928) and all possess similar plant communities, particularly near exposed granite rock. Burbanck and Platt (1964) note the similarities between the Piedmont granite and the Llano Uplift of Texas stating "although the species are different, the types of plants and the stages of succession on exposed granite and accumulated gravel at Enchanted Rock, Texas…are similar to conditions in Georgia." Walters and Wyatt (1982) echo this sentiment by stating "that granite outcrops provide similar types of microenvironments despite major differences in the climate and surrounding vegetation of each region."

While the granitic regions west of the Mississippi River (Llano Uplift, Wichita Mountains, and Arbuckle Uplift) share similar geology and microenvironments to that of the Piedmont granite, their floras are quite different (Walters & Wyatt 1982). This lack of similarity in characteristic and endemic species between the eastern and western granitic outcrops "suggests that each region contains a unique group of plants independently derived from the native plants of that region" (Walters & Wyatt 1982). When examined at the generic level this is not necessarily the case though, with several genera having "highly specialized representatives in both regions" (Walters & Wyatt 1982).

These widely separated regions possess similar floras, including disjunct taxa such as *Cyperus granitophilus,* as a result of a shared flora during the Tertiary period. The Madro-Tertiary Geoflora of western and southwestern North America shows remarkable floristic similarities to that of the Llano Uplift, Wichita Mountains, Arbuckle Uplift and Piedmont granite rock outcrop floras (Walters & Wyatt 1982). Warmer and drier climates during the Late Tertiary allowed plants from western and southwestern North America to expand their ranges into the southeastern United States (Braun 1955). Thus, it is likely that the Llano Uplift, Wichita Mountains, Arbuckle Uplift, and Piedmont once had a shared flora and that flora was adapted to warmer and drier conditions than what exist today across most of the region. Cooler and wetter temperatures in the Pleistocene subsequently forced xerophytes in the Southeast to take refuge on rock outcrops. Once isolated, subsequent speciation would result in narrowly restricted endemics within each system, such as *Isoëtes lithophila* in the Llano Uplift and *I. melanospora* Engelm. in the Piedmont.

Alternatively, the absence of species divergence after isolation would result in highly disjunct populations. This distribution pattern is not atypical for ecological endemics with highly restrictive specificity to a single substrate. This is seen with *Cyperus granitophilus, Eriocaulon koernickianum,* and *Isoëtes piedmontana* (N.E. Pfeiffer) C.F. Reed on granite outcrops and *Isoëtes butleri* Engelm. (Taylor et al. 2012), *Gratiola quartermaniae* D. Estes (Taylor & O'Kennon 2014), and *Oenothera macrocarpa* Nutt. ssp. *macrocarpa* (Kartesz 2014) on limestone outcrops. Additionally, environmental differences between outcrop communities and the surrounding habitats is markedly more intense in the Piedmont where the incident radiation, temperatures and high levels of evapotranspiration are drastically more severe on the rock outcrops than the surrounding habitats. Warmer and drier overall climates in Texas and Oklahoma result in a less extreme environmental difference between outcrops and surrounding vegetation, less isolation from congeners, and a lower degree of endemism (Walters & Wyatt 1982).

Voucher Specimens. **U.S.A. OKLAHOMA. Comanche Co.:** Elk Mountain, Wichita Mountain Wildlife Refuge, 34.725819 -96.721114, 19 Jun 2015, *O'Kennon, Taylor, Jensen, & Rylander, 28463* (BRIT); Northwest Sunset Peak, 21 May 1983, *Rose 85* (OKL); wet, sandy shoreline, Quanah Parker Lake, Wichita Mts., 2 Jun 1949, *Penfound P-197* (OKL); sandbar, head of Lake Elmer Thomas, 9 Jul 1948, *Penfound P-54* (OKL); Wichita Mts. Wildlife Refuge, Sugar Creek, open prairie near North boundary, 29 Jul 1942, *Rouse 405* (OKL); growing in soil collected among granite boulders near top of Mt. Scott, Wichita Mts, 4 Jul 1941, *Waterfall 2925* (OKL); clay and shale on granite with a mixed grass – sedge association, N of Mt. Scott about 1 mi E of Meers, Wichita Mts., 4 Jul 1941, *Waterfall 2904* (OKL); Medicine Park, 20 Oct 1934, *Bradbury 593* (OKL); s.d., *Stevens 1330* (OKL); s.d., *Stevens 1358* (OKL). **Greer Co.:** at edge of small mountain near granite, 17 Jun 1913, *Stevens 1027* (OKL). **Johnston Co.:** granite rock at 10 Acre Rock, 34.328989 -96.762469, 13 Jun 2015, *O'Kennon 28420* (BRIT); granite rock area W of town of Mill Creek, 19 May 1967, *Taylor & Taylor 3690* (OKL). **TEXAS. Burnet Co.:** Granite Mountain along Farm Road 1431, 1.8 mi W of F.M. 1431 and U.S, 281, W of Marble Falls, 7 Jun 1988, *Urbatsch 4791* (BRIT); growing in loose small granite rocks, Granite Mountain, 16 Jun 1946, *Cory 12729* (SMU). **Gillespie Co.:** Enchanted Rock State Natural Area, in moist granitic glade south of Little rock, N30.495971, W98.829125, 26 Jun 2014, *O'Kennon, Taylor, & Rehman 26146* (BRIT); Enchanted Rock State Natural Area, in moist granitic grus, S of Little Rock, N30.4959566, W98.8291267, 16 Jul 2014, *Taylor, O'Kennon, & Rehman 2852* (BRIT); in granite gravel on outcrop near Coal Creek, N of Willow City, 10 Jul 1958, *Correll & Johnston 19582* (TEX-LL); in shallow depressions in granite on Bear Mt., just N of Fredericksburg, 29 Jun 1957, *Correll & Johnston 17258* (TEX-LL); 5 Aug 1940, *Strandtmann s.n.* (TEX-LL). **Llano Co.:** Enchanted Rock State Natural Area, vernal pool on Enchanted Rock, N30.506892, W98.81962436, 21 Oct 2014, *Taylor & O'Kennon 2935* (BRIT); granite dike E of Enchanted Rock, N30.51247, W98.8026, 19 Sep 2014, *Taylor & O'Kennon 2908* (BRIT); drainage over granite, N30.50604, W98.8348, 18 Sep 2014, *Taylor & O'Kennon 2885* (BRIT); vernal pool on West Rock, N30.50006, W98.8229, 17 Sep 2014, *Taylor & O'Kennon 2860* (BRIT); Enchanted Rock SNA, N30.500257, W98.819718, 15 Jul 2014, *Taylor, O'Kennon & Rehman 2776* (BRIT); Enchanted Rock State Natural Area, in moist granitic sand along margin of Sandy Creek that runs near the southern and eastern base of Enchanted Rock, N30.510462, W98.804992, 15 Jul 2014, *O'Kennon, Taylor, & Rehman 26142* (BRIT); Enchanted Rock SNA, Moss Lake, 14 Jul 2014, *O'Kennon, Taylor, & Rehman 26145* (BRIT); Enchanted Rock SNA, along moist bank of Moss Lake, N of Enchanted Rock, N30.50888, W98.825086, 4 Oct 1990, *O'Kennon 8128g* (BRIT); 9.6 mi SW on FM 2323 from its jct with TX 16, then S ca 100 m on an unnamed paved rd, E side of rd, SW of Llano, granitic outcrop between the road and fence, associated species other *Cyperus, Leptochloa, Digitaria, Bouteloua, Tripogon*, and *Bothriochloa*, 26 Sep 1987, *Wipff 563* (TEX-LL); granite outcrop 1.4 km W on Ferguson Rd from intersection of Ferguson Rd and RR 2147 at Horseshoe bay, 11 Aug 1979, *Walters 1000* (TAMU); granite outcrop 3.4 km N on W side of RM2241 from the intersection of RM 2241 and U.S. Hwy 21 at Bluffton, 18 Jun 1979, *Walters 681* (TAMU); common sedge in many of the vernal pools on the summit of Enchanted Rock, 2 Oct 1976, *Butterwick & Smith 3376* (TEX-LL); common annual sedge in vernal pools on summit of Enchanted Rock, 24 Jul 1976, *Butterwick & Lamb 3020* (TEX-LL); Watch Mountain, granite outcrop 17.2 km W on N side of Inks Ranch Rd, from the intersection of Inks Ranch Rd and U.S. Hwy 16, 13 Jun 1974, *Walters 496* (TAMU); Enchanted Rock, 20 Aug 1936, *Tharp s.n.* (BRIT); granitic areas, 5 Aug 1931, *Wolff 3157* (BRIT); Enchanted Rock, 11 Jun 1930, *Whitehouse & Tharp s.n.* (TEX-LL); Enchanted Rock, Jul 1892, *Nealley 80* (TEX-LL). **Mason Co.:** Mason Mountain WMA, in moist cracks in granite, N30.826464 W99.220053, 14 Aug. 2012, *O'Kennon, Taylor, & Rehman 25348* (BRIT); granite outcrop and sandy creek bottom, 14.2 mi E of Mason by highway TX 29, local in thin sand over rock, 16 Aug 1989, *Carter 8214* (SAT, VSC); granite outcrop 2.6 km E on S side of RM

1222 from intersection of U.S. Hwy 87 and RM 1222 at Camp Air, *Walters 441* (TAMU); granite outcrop 2.7 km S on U.S. Hwy 87 from intersection of U.S. Hwy 87 and RM 1222 at Camp Air, W 0.2 km, 11 Jun 1979, *Walters 424* (TAMU).

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ANNOUNCEMENT

THE 2015 APPLICATIONS FOR THE DELZIE DEMAREE TRAVEL AWARD

Applications for the 2015 Delzie Demaree Travel Award should include a letter from the applicant telling how symposium attendance will benefit his/her graduate work and letter of recommendation sent by the major professor. Please send letters of application to: Dr. Donna M.E. Ware, P.O. Box 8795, Herbarium, Biology Department, The College of William and Mary, Williamsburg, Virginia 23185-8795, U.S.A. 1-757-221-2799; Email: ddmware@wm.edu. Applications may be sent to: Barney Lipscomb, 1700 University Drive, Fort Worth, Texas 76107-3400, U.S.A. 1-817-332-7432; Email: barney@brit.org. The period for receiving applications will end three weeks prior to the date of the symposium if a sufficient number of applications are in hand at that time. Anyone wishing to apply after that date should inquire whether applications are still being accepted before applying. The Systematics Symposium dates for 2015 are 8–10 October 2015 (dates tentative and subject to change).

The Delzie Demaree Travel Award was established in 1988 honoring **Delzie Demaree** who attended 35 out of a possible 36 symposia before he died in 1987. Delzie Demaree was a frontier botanist, explorer, discoverer, and teacher. His teaching career as a botanist began in Arkansas at Hendrix College in 1922. He also taught botany at the University of Arkansas, Navajo Indian School, Yale School of Forestry, Arkansas A&M, and Arkansas State University at Jonesboro where he retired as professor emeritus in 1953. One of the things he enjoyed most as a botanist was assisting students with their field botany research.

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PHYTOGEOGRAPHICAL RELATIONSHIPS AND ANALYSIS OF THE FLORA OF SOUTH-CENTRAL TEXAS, U.S.A.

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ABSTRACT

A flora of the elevated portion of Edwards Plateau and western half of the Llano Uplift in South-Central Texas (SC TX flora) was studied from a biogeographical perspective. A checklist of the designated flora was extracted primarily from the "Floristic Synthesis of North America" and data concerning general distribution of the taxa were obtained from the literature and online databases. Phylogenetic literature was searched to find relationships, patterns of migrations, and geographical connections of the species of major clades. Taxonometric and geographic spectra of the SC TX flora were obtained and compared with those for the flora of Big Bend Region (BB), Texas. There are 1619 native species of 626 genera and 149 families in the SC TX flora. These species were classified into 21 geographic (floristic) elements. Herein is presented a checklist accompanied by the geoelement descriptions and the taxonometric and geographic analyses of the flora. The flora, being on the boundary of two floristic subkingdoms and two regions, has a complex pattern of connections. Among five most specious families, the Asteraceae and Euphorbiaceae have half of their species in the local clades which diversified after transatlantic long distance dispersals. The rest of the spurges and about 70% of the grasses and sedges have tropical/subtropical connections. Almost two thirds of the Fabaceae have connections to SE N American/Madrean/Mesoamerican, Tethyan or S American radiations. The largest geoelement in the flora is comprised of 236 E North American species. The entire North American Atlantic Region is represented by 679 species (42% of the flora). Only 11% of the Big Bend flora species are in this group. The Holarctic Subkingdom in general is represented by 794 species (49% of the flora). The Western Region/Madrean Subkingdom has 450 species (28% of the flora), followed by the Madrean/Neotropical Region with 212 species (14% of the flora). There are 132 differential genera in the SC TX flora not found in the Big Bend flora, including 54 tropic/subtropical, 34 temperate N Hemispheres, 14 E North American, and 12 SC/SW USA-N Mexico genera. Higher numbers in mesophyllous genera and more connections with the North American Atlantic Region are evident from the family and generic spectra of the SC Texas flora, while the Big Bend flora spectrum has more species of the xeric genera native to southwestern North America. In general, southern and eastern connections prevail in the SC TX flora. Most characteristic scenario in taxonomically significant groups shows local diversification after transatlantic crossings of the ancestral species from the Old World, as well as S/N American bidirectional migrations, whereas most oligotypic and monotypic genera include relictual species of tertiary Lauroasian genera, best preserved in the southeastern North America, or species of tropical genera extending to the southern boundary of U.S.A.

RESUMEN

Se estudió la flora de una porción elevada del Edwards Plateau y oeste de la elevación del Llano en el centro-sur de Texas (SC TX flora) desde una perspectiva biogeográfica. Se extrajo primariamente un catálogo de dicha flora a partir de la "Floristic Synthesis of North America" y se obtuvieron datos de la distribución general de los taxa a partir de la bibliografía y de databases online. Se examine la bibliografía filogenética para hallar relaciones, patrones de migraciones y conexiones geográficas de las especies de los clados mayores. Los espectros taxonométricos y geográficos de la flora SC TX se obtuvieron y se compararon con los de la flora de la región Big Bend (BB), Texas. Hay 1619 especies nativas de 626 géneros y 149 familias en la flora SC TX. Estas especies se clasificaron en 21 elementos geográficos (florísticos). Se presenta aquí un catálogo acompañado de descripciones del geoelemento y de análisis taxonométricos y geográficos de la flora. La flora, situada en la frontera de dos subreinos florísticos y dos regiones, tiene un patrón complejo de conexiones. Entre las cinco familias con más especies, las Asteraceae y Euphorbiaceae tienen la mitad de sus especies en los clados locales que se diversificaron después de las dispersiones a larga distancia transatlánticas. El resto de las euforbias y sobre el 70% de las gramíneas y ciperáceas tienen conexiones tropicales/subtropicales. Casi dos tercios de las Fabaceae tienen conexiones con radiaciones con SE N Americanas/Madreanas/Mesoamericanas, Tethyanas o S Americanas. El mayor geoelemento de la flora comprende 236 especies del E Norte Americano. La Región entera Norte Americana Atlántica está representada por 679 especies (42% de la flora). Solamente el 11% de las especies de la flora Big Bend están en este grupo. El subreino Holártico en general está representado por 794 especies (49% de la flora). La Región Oeste /Subreino Madreano tiene 450 especies (28% de la flora), seguida por la Región Madrean/Neotropical con 212 especies (14% de la flora). Hay 132 géneros diferenciales en la flora SC TX que no se encuentran en la Big Bend, incluyendo 54 géneros tropicales/subtropicales, 34 del hemisferio N templado, 14 E Norte Americanas, 12 SC/SW USA-N México. Los números más altos en los géneros mesófilos y más conexiones con la Región Norte Americana Atlantica son evidentes en los espectros de familias y géneros de la flora SC Texas, mientras que el espectro de la flora Big Bend tiene más especies de los

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géneros xéricos nativos del suroeste de Norte América. En general, las conexiones con el sur y este prevalecen en la flora SC TX. El escenario más característico en los grupos más significantes taxonómicamente muestra diversificación local después del paso transatlántico de las especies ancestrales desde el Viejo Mundo, así como las migraciones bidireccionales S/N Americanas migraciones, mientras que los géneros más oligotípicos y monotípicos incluyen especies relícticas de géneros del terciario Lauroasiático, mejor preservados en el sureste de Norte América, o especies de géneros tropicales que se extienden hasta la frontera sur de Estados Unidos.

INTRODUCTION

Comparative floristic analysis has long been one of the major tasks for phytogeographers from different parts of the world. Well defined and carefully analyzed regional floras can be used for comparison with other floras and elucidation of the connections among them. The analysis is preceded by the grouping of the species of a flora into diverse floristic elements: geographic, ecological, historic, etc, depending on the goal. A natural flora can be viewed as a section of, or a probe into, the ever changing continuum of plant cover. It is a section of a particular size in space and time and as such it can be used for the clarification of its composition and how it changes through time. For chorionomic regionalization, which seeks to delineate natural geographic areas with distinct floras, it should be delimited by natural barriers. Such floras are characterized by specific assemblages of endemic taxa of particular rank, depending on the rank of the chorion (Takhtajan 1986; Kamelin 1973; 1990; 1998; 2010). To define biogeographical regions, different authors used cluster analysis, principal component analysis, and other statistical techniques (McLaughlin 2007; Finnie at al. 2007; Born et al. 2007; Linder et al. 2012) or used the phylogenies of particular taxonomic groups for parsimony analysis of endemicity (Morrone et al. 1999; Katinas et al. 2004). A different approach to floristic analysis utilizes more loosely defined boundaries of a flora to focus not on its regionalization but on the presence of its extant taxa in the region and their phylogenetic relationships with sister taxa in other floras (Galley & Linder 2006), especially on the taxa with intercontinental disjunctive patterns (Thorn 2004; Renner 2004; Donoghue & Smith 2004; Wen & Ickert-Bond 2009; Olmstead, 2013). With the wealth of now available published phylogenies and historical biogeographical analyses, some repetitive patterns of disjunctions, dispersals, vicariance, and extinctions emerge among many non-related taxonomic groups of a given flora. This paper focuses on the search of such repetitive patterns of disjunctions in the phylogenetic literature for the taxa of a sample flora in South-Central Texas. For this purpose, a flora in South-Central Texas, which includes more elevated parts of the Edwards Plateau and the western Llano Uplift in the natural regions 7 and 8 (Fig. 1), is loosely delineated and will be presented and analyzed in this work. It is not our intention to reconsider the natural regions in the area, as it is a separate task.

Another purpose of this paper is to compare two almost adjacent floras in Texas: the floras of South-Central Texas (SC TX), which is the subject of this study, and the flora of Big Bend Region (BB), in natural region 11 (Fig. 1) analyzed in A. Saghatelyan (2009). Depending on the chorionomic system we use, SC TX falls into two different regions. It is a part of the North American Prairies Province of the Atlantic North American Region in the chorionomy of Cronquist (1982) and Takhtajan (1986) accepted in this paper (Fig. 2). According to this system, SC TX falls into a different region than BB, which is a part of the Madrean Region. Alternatively, it is a part of the Southwestern Region of the chorionomic system of S. McLaughlin (2007), which includes the Great Plains Province. As such, the SC TX flora would be placed together with the BB flora in the Southwestern Region. Thus, a detailed floristic analysis can support one of those placements, depending on its species connections and the degree of similarity of the two sample floras.

GEOGRAPHIC SETTING

The Edwards Plateau of SC Texas is a plateau east of the continental divide, sloping gently eastward, but steeper and dryer at the western margin. Its elevation ranges from 450 ft to 3000 ft. The dissected southern and eastern half of the Edwards Plateau is known as the Texas Hill Country. Its surface consists almost entirely of outcrops of Cretaceous limestone. A relatively small area in the north central margin of the Edwards Plateau is known as the Granitic Central Basin, or Llano Uplift. In this area the Cretaceous limestone has been removed by erosion. The exposed rocks are largely granitic and gneissic. The Balcones Escarpment at the southeastern

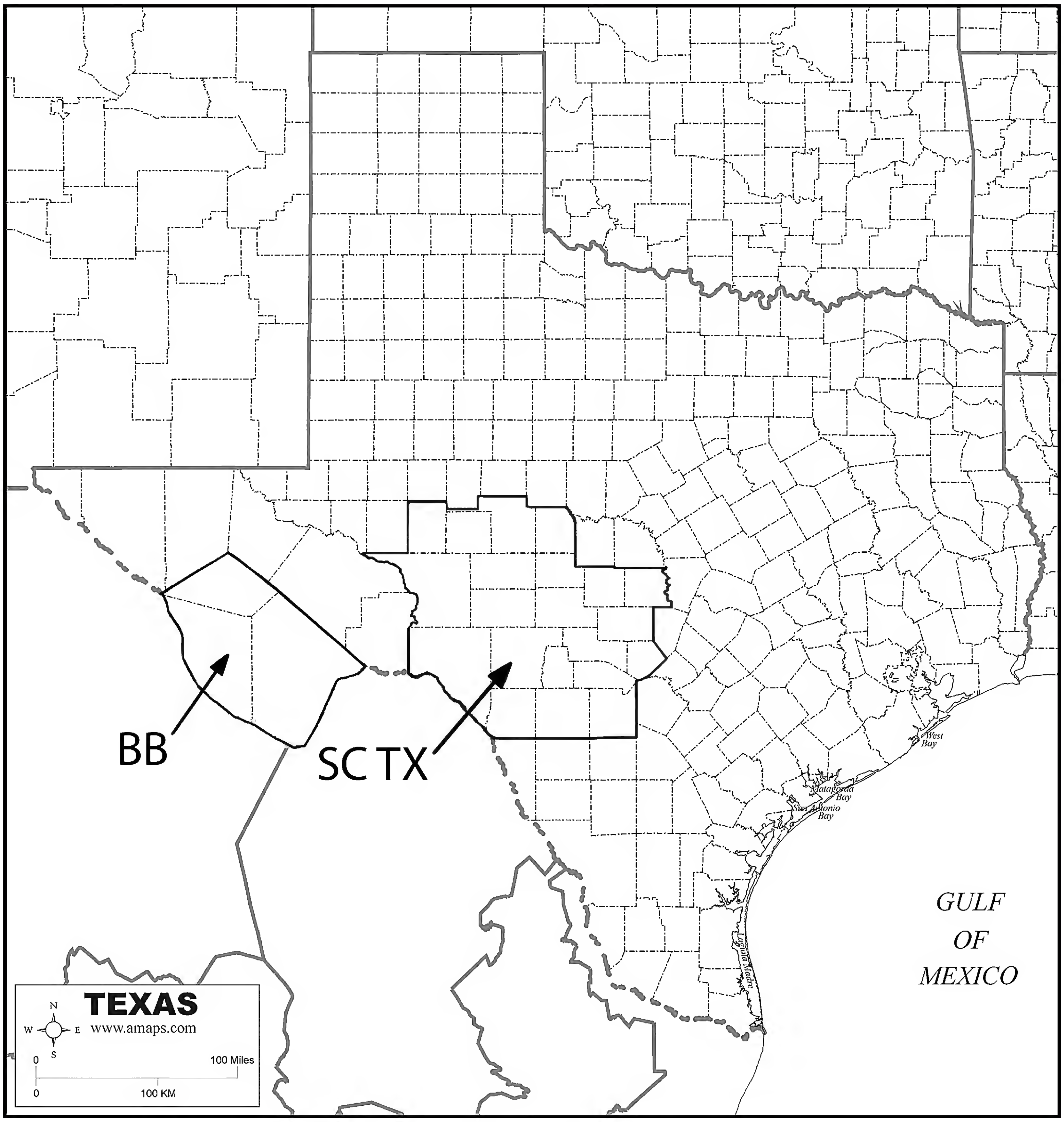
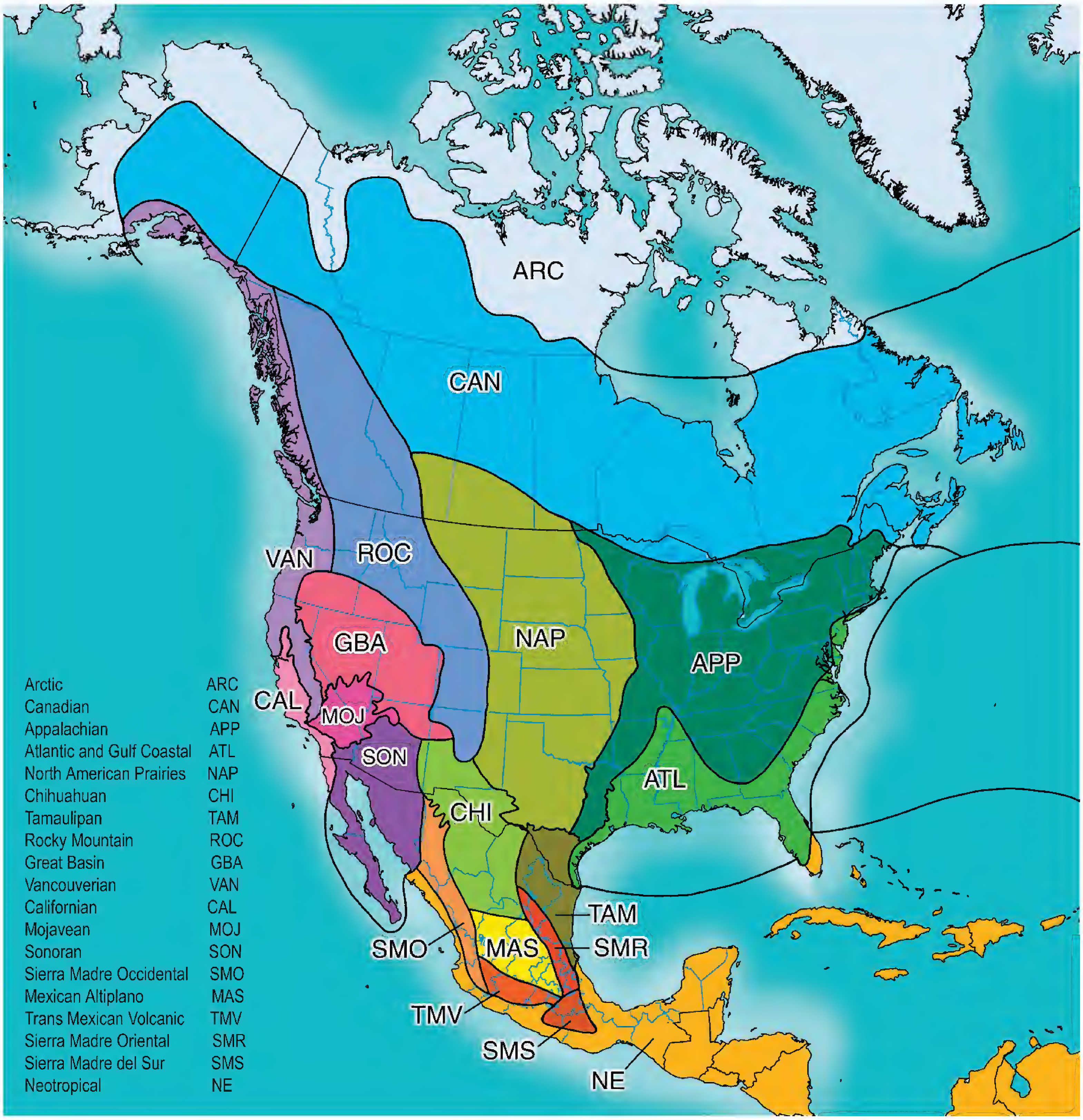


Fig. 1. Texas county map with the study area of the South Central Texas flora (SC TX) and the Big Bend area (BB) outlined by a bold contour. The map is courtesy of Texas Parks and Wildlife and was modified in Photoshop by Mike Karabegov.

edge of the Edwards plateau seems to be a floristic barrier (MacRoberts & MacRoberts 2008). The study area covers the elevated central part of the mostly limestone Edwards Plateau east of the Pecos River and the western part of the granitic Llano Uplift. Most of its land surface has been exposed continuously for occupation by terrestrial biota for at least 65,000,000 years (Correll & Johnston 1970) and has subhumid subtropical climate.

The study area is outlined on the map (Fig. 1) and includes the following counties: Bandera, Concho, Crockett, Edwards, Gillespie, Irion, Kendall, Kerr, Kimble, Kinney, Llano, Mason, Medina, Menard, Reagan, Real, Schleicher, Sutton, Tom Green, Uvalde, and Val Verde. The Edwards Plateau environments and vegetation are well known (Amos & Gehlbach 1988). The “original” vegetation was grassland or more commonly a type of open temperate grassland, with shrubs and low trees along rocky slopes (Correll & Johnston 1970;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Canadian CAN
Appalachian APP
Atlantic and Gulf Coastal ATL
North American Prairies NAP
Chihuahuan CHI
Tamaulipan TAM
Rocky Mountain ROC
Great Basin GBA
Vancouverian VAN
Californian CAL
Mojavean MOJ
Sonoran SON
Sierra Madre Occidental SMO
Mexican Altiplano MAS
Trans Mexican Volcanic TMV
Sierra Madre Oriental SMR
Sierra Madre del Sur SMS
Neotropical NE

Fig. 2. Floristic provinces/areas of endemism of North America. Regional schema adapted from Takhtajan (1986) as published in Thorne (1993). The areas were drawn in Photoshop by Alice Tangerini on a base map from ArcMap8.2 with a North American Lambert conformal conic projection. The map was published in Katinas et al. (2004) and is used with permission of Missouri Botanical Garden Press and the authors.

Stanford 1976; Hatch et al. 1990). The floristic geography of woody and endemic plants was analyzed by Amos and Rowell (1988).

Here is presented a checklist and detailed analysis of the SC TX flora, including the study of general distribution outlines of its species and genera as well as their classification into geographical elements. This information coupled with the phylogenetic literature data will help to reveal connections of the flora to other floras and possible migration routes of its ancestral species.

MATERIALS AND METHODS

A checklist of the flora of the study area in SC Texas, including the Edwards Plateau and western part of the

Llano Uplift, was compiled using primarily the Synthesis of the North American Flora (Kartesz 2013). The non-native species were excluded. Twenty-seven sandy land species reported outside of the Edwards Plateau ecoregion in Medina County, only from the Carrizo Sand south of the Balcones Escarpment, were also excluded. Taxonomic counts of the families, genera, and species were performed. Distributional and other data was obtained from the Synthesis of the North American Flora (Kartesz 2013), Tropicos (Tropicos.org.), Flora of North America and Digital Flora of Texas databases, literature on Texas flora (Correll & Johnston 1970; Johnston 1990; Turner et al. 2003; Diggs et al. 1999), many online databases on different taxonomic groups (like G. Nesom, Astereae database), and other literature sources. After revealing general distribution outlines for each species of the flora, congruent ranges of two or more species were classified into geographic elements using the classification system of geographic elements (Saghatelyan 2009) developed on the example of the BB flora. Each species was thus referred to and treated as a particular geographic element or geoelement (Saghatelyan 1997a, b). The distributional data on all the genera were retrieved from Wielgorskaya (1995), Mabberley (1997), the Flora of North America, Flora of China, and online sources. The genera were classified into 19 groups based on their distribution outlines. The species list (Appendix 1) for the above-mentioned counties was compiled with the major objective of defining the geoelements and follows the nomenclature accepted in Kartezs (2013), with the exception of Liliales and Asparagales, which follow APG. The unidentifiable ranges of a few species are noted with a question mark in the checklist. After analyzing the SC TX flora, the taxonomic and geographic compositions of the flora were compared with those of the BB flora. A special attention was given to phylogenetic literature search to clarify the relationships of significant in the flora taxonomic groups and patterns of vicariance and/or migration.

TAXONOMETRIC ANALYSIS OF MAJOR FAMILIES

There are 1619 species in 626 genera and 149 families in the SC TX flora (Appendix 1). Specific and generic richness of the largest families is presented in Table 1. First ten largest families comprise 859 species or 53% of the flora. The family spectrum is close to that of the BB flora. However, Fabaceae, Euphorbiaceae, Cyperaceae, Rosaceae, and Apiaceae are more speciose in the SC TX flora, while Cactaceae, Boraginaceae, and Brassicaceae have a higher percentage of species in BB.

The largest family Asteraceae has 232 species in 98 genera in the SC TX flora. Different clades of the compositae metatree (Funk et al. 2009) have the following numbers of species in the flora. The flora includes only four species of the South American Mutiseae clade, which have the Sonoran Province/East Madrean ranges. North American Cardueae have only eight species in the flora. This latter group diverged from Plio-Pleistocene or later (Hellwig 2004) diversification in the West Asian-Mediterranean thistle clade and represents a recent monophyletic radiation to North America (Barres et al. 2013; Funk et al. 2005; 2009).

Fourteen of the 15 species of the Lactuceae and Vernonieae in the flora have the East Prairie-Eastern North American ranges. This concentration of the Lactuceae in the eastern North America supports a probable trans-Atlantic crossing from the Mediterranean. While Lactuceae may have arrived from the Mediterranean, the dispersal in Vernonieae was from tropical Africa to South America and then from South to North America, with Meso/Central America playing an important role (Keeley et al. 2007; Keeley et al. 2013). The small tribe of Moquinieae is in a clade with Vernonieae in the Atlantic SE Brazil, while North American members of Vernonieae are more highly nested in that clade (Funk et al. 2005; Funk et al. 2009).

Asteroideae, the largest subfamily in North America, starts with the global tribe Senecioninae, richly represented (with 61 sp. of *Senecio* and 54 sp. of *Packera*) in western North America, but with only seven species in the SC TX flora. The Gnaphalieae (eight sp.) and Anthemideae (two sp.) are also scarce in SC TX while being highly diverse in the western North America. For example, the North American endemic *Artemisia* group with 58 species in western North America has only one species in the SC TX flora. The group diverged from Asian ancestors by the Late Miocene (González et al. 2011) and arrived via Beringia. The pattern of distribution of the species of Senecioninae in North America resembles that of the genus *Artemisia* and points to a probability of the Beringia crossings.

Table 1. Edwards Plateau (**EP**) and Big Bend (**BB**) flora largest families. The list is ordered by the number of Edwards Plateau species in each family, and percentages are relative to the entire flora.

Largest Families	EP species (%) / genera	BB species (%) / genera
Asteraceae	232 (14.3) / 98	230 (14.5) / 107
Poaceae	199 (12.2) / 65	202 (12.7) / 63
Fabaceae	120 (7.4) / 41	107 (7.1) / 37
Cyperaceae	69 (4.2) / 11	40 (2.5) / 10
Euphorbiaceae	68 (4.1) / 12	59 (3.7) / 10
Cactaceae	40 (2.5) / 13	59 (3.7) /17
Brassicaceae	37 (2.3) / 14	43 (2.7) / 21
Lamiaceae	36 (2.2) / 11	38 (2.4) / 11
Plantaginaceae	34 (2.1) / 11	29 (1.8) / 13
Solanaceae	28 (1.7) / 10	32 (2.0) / 10
Pteridaceae	27 (1.7) / 7	33 (2.1) / 8
Rosaceae	26 (1.6) / 10	12 (0.8) / 9
Malvaceae	24 (1.5) / 12	24 (1.5) / 12
Apiaceae	24 (1.5) / 18	7 (0.3) / 5
Onagraceae	24 (1.5) / 3	28 (1.8) / 4
Boraginaceae	22 (1.4) / 11	33 (2.1) / 9
Asclepiadaceae	21 (1.3) / 4	23 (1.5) / 4

Astereae have 72 species in the SC TX flora. Conyzinae have 15 species and are a North American group with the basal taxa being *Erigeron* species from southwestern N America (Nesom 1994; Noyes & Rieseberg 1999). The Solidagininae have 11 species all with ranges in the eastern North America. This is where the center of diversity of the genus *Solidago* lies. Broadly North American genera *Symphyotrichum* and *Heterotheca* have 14 species in the flora. Remaining two thirds of the Astereae species have southern or western connections. Among them are 25 species of the genera *Baccharis, Gutierrezia, Laennecia*, *Grindelia, Isocoma,* and *Croptilon,* centered in Mexico, western or southern North America and South America. All North American Astereae are members of a strongly supported clade, with basal Astereae being predominantly woody taxa from Africa, Australia, and South America (Noyes & Rieseberg 1999). African genera form a basal clade in the tribe Astereae along with the Chinese genus *Nannoglottis* and South American and New Zealand genera. The latest diverging African clade, subtribe Grangeinae, is sister to the Eurasiatic subtribe Bellidinae, and together they are sister to the Astereae crown lineages of Australasia-Asia and South and North America (Brouillet et al. 2009).

Inulea have only two species of the tropical-warm temperate genus *Pluchea* in the flora.

Heliantheae s.l. is the most speciose group of the Asteraceae in the flora. An eastern Cuban genus *Feddea* was shown to be sister to the Heliantheae s.l., and the New World *Feddea*/Heliantheae s.l. group was shown to be sister to the mostly Old World (predominantly in E Africa) tribe Athroismeae (Cariaga et al. 2008). Funk et al. (2009) do not exclude the possibility of a direct Old World to New World dispersal of the American clade of Heliantheae.

The core Heliantheae Alliance begins with Helenieae.The flora has 20 species of Helenieae with the south-central or southeastern North American ranges, including one species of the genus *Marshallia*. *Marshallia* is sister to the rest of Helenieae and grows in mostly mesic habitats in south-central/southeastern United States. This supports the above mentioned proposed dispersal route for Heliantheae from the Old World.

The Coreopsideae have nine species with similar ranges.

The Eupatorieae are concentrated in Mexico and Central and South America; they have 14 species in the flora. *Eupatorium* had initial divergence in North America and shares a common ancestor with *Liatris* (Schmidt & Schilling 2000). The Liatrinae is essentially restricted to the eastern and south-eastern United States (Nesom 2005). Remaining 91 species of the Heliantheae Alliance in the flora have the Chihuahuan-Tamaulipan, Madrean, or Comanchian ranges, or broader south-central North American-E Prairie distribution.

Thus, a majority of the Asteraceae species of the SC TX flora belong to the largest North American Heliantheae Alliance. Together with the species of the Astereae, Inuleae, and Vernonieae they have mostly southern connections, especially in SE/SC North America or Central/South America. For present-day Asteraceae composition of SC TX flora, long distance dispersals of the ancestral taxa from Mediterranean to Mesoamerica/North America or from Africa to South America to North America were much more important than Beringia crossings. The groups that have richly diversified in Western North America after a Beringia crossing, have only a few species in the SC TX flora.

Poaceae, with 199 species of 65 genera in the flora, is the second largest family. Its species, as grasses in general, have broad geographic ranges. The subfamilies characteristic to tropical/warm temperate latitudes, especially Chloridoideae (71 sp.) and Panicoideae (61 sp.), have the majority of the species and eight largest grass genera in the flora. Major centers of diversity of these genera are in Mexico and Mesoamerica. The ranges of their species found in the flora are mostly in North American southwestern, south-central or, for a few, in southeastern parts. To the contrary, the mostly north temperate subfamily Pooideae has only 29 species in the flora. These Pooideae genera are small in the flora, monotypic or ditypic, with the largest one having only eight species.

Fabaceae has 120 species of 41 genera and is in third place in the SC TX flora. Compared to the legumes of the Big Bend flora (Saghatelyan 2009), there are seven more genera in SC TX: E Asian-E North American-South American disjunctive genus *Gleditsia,* four tropical/subtropical genera, *Bauhinia, Clitoria, Neptunia,* and *Zornia,* and two E North American genera of Papilionoideae, *Baptisia* and *Apios*. Caesalpinioideae of the SC TX flora have eight genera and 15 species with mostly E North American, SC TX, or Chihuahuan-Tamaulipan ranges. For the genus *Gleditsia* of E Asian origin both the mid-Miocene N Atlantic Land Bridge crossing (Tiffney 1985; Schnabel & Wendel 1998; Lavin et al. 2000) and the Bering Land Bridge crossing (Schnabel et al. 2003) were proposed. The Atlantic crossing seems more plausible due to the strong macrofossil record for *Gleditsia* in Europe. According to Mai (1995), *Gleditsia* was present in the savanna type vegetation in the Miocene of southern Europe, and its presence had decreased all over Europe in the Pleistocene. Other thermophyllous genera, like *Gymnocladus* and *Cercis,* exhibit a similar pattern (Mai 1995). According to a molecular phylogeny of *Cercis* (Fritsch & Cruz 2012), North American species are sister to the western Eurasian species with strictly east-to-west vicariance. It was inferred that the ancestor in which this divergence occurred in the mid-Miocene was xerophytic and used the Miocene North Atlantic corridor for semi-arid plants. Basalmost Caesalpinioideae (*Gymnocladus, Cercis, Ceratonia, Gleditsia,* and *Senna*) had a strong participation in the Tertiary assemblages of subtropical floras of littoral type (Mai 1995). Schrire et al. (2005:405) also conclude: “Such older northern temperate diversifications thus reflect a Tethyan-wide Tertiary tropical dry forest distribution which existed prior to temperate conditions being superimposed on these areas.”

In North America, the genera *Senna, Bauhinia, Chamaecrista,* and *Parkinsonia* of the Succulent Biome of Schrire et al. (2005), which has pantropical disjunct distribution, are restricted to south or southeastern United States and Mexico (Kartesz 2013). This suggests transatlantic peri-Tethyan migrations for the pantropical genera (*Parkinsonia*) and south/north migrations for the mostly tropical American genera (*Chamaecrista*). The Grass Biome (Schrire et al. 2005) genus *Hoffmannseggia* is amphitropically disjunct due to the long distance dispersals from South to North America (Simpson et al. 2005). In the United States its species grow in the southwest, which is common among other amphitropically disjunct genera. The genus *Pomaria* of the Grass Biome of Schrire et al. (2005) also has amphitropical disjunction with extension to the western Prairie Region. It had dispersal from southwestern United States and adjacent Mexico to southern Africa and second dispersal from North America to temperate South America (Simpson et al. 2006).

Mimosoideae in the SC TX flora have 32 species in seven genera, all with southern connections. Many of these species are common with the Big Bend flora (Saghatelyan 2009). However, the Madrean and Gulf Coastal species of the Mimosoideae are more numerous in the SC TX than in the BB flora. The Succulent Biome species comprise two thirds of the Mimosoideae in SC TX. One-third of the Mimosoideae represent the Grass Biome of the Western hemisphere.

Papilionoideae have 84 species in the flora with the ranges mostly in the N American Atlantic Region: E North American, Comanchian, E Madrean, Mesoamerican-Madrean, SC North American, E Prairie, and Tamaulipan. To the contrary, the species of papilionoids in the Big Bend flora have mostly western and southwestern North American ranges.

The basal Papilionoids in the SC TX flora are represented by two out of the three distinct lineages of the Sophora Alliance. These two lineages have two monotypic genera in the flora. One of them, the Mexican-Mesoamerican genus *Styphnolobium,* is related to E Asian-E North American disjunctive genus *Cladrastis,* while the other one, a Madrean genus *Calia* (where *Sophora secundiflora* was moved), is related to the South American genus *Holocalyx* (Schrire et al. 2005). The third lineage is comprised of Eurasian, pantropical, and south temperate representatives of the genus *Sophora* (Heenan et al. 2004) and is absent from the flora.

The pantropical dalbergioid clade is represented by only one species of the genus *Zornia* in the flora of SC TX. Dalbergioids are sister to the Amorpheae clade, which is confined to the arid regions of temperate and tropical North America (Wojciechowski 2003). The Amorpheae have three genera and 21 species in the SC TX flora, including 18 species of a large and more widespread genus *Dalea*. Genus *Lupinus* (one sp.), whose ancestor arrived from the Macaronesian-Mediterranean Region to the New World, represents South African based temperate (Tethyan) radiation of the Genisteae clade of core genistoids (Schrire 2005). One more core genistoid genus in the flora, *Baptisia* (E North American), allies with the North American genus *Thermopsis* (mostly western North American) in the Thermopsideae clade (Wang et al. 2006). Interestingly, the East Asian *Thermopsis* allies with the monotypic Canarian genus *Anagyris* and the Sino-Himalayan genus *Piptanthus*. Wang et al. (2006) suspect that there was some intercontinental exchange of species in the genus *Thermopsis* around the Bering Strait which started the divergence in that genus.

The Phaseoloids in the SC TX flora have eight genera of the Grass Biome affiliation, with pantropical or amphi-atlantic disjunctions, and two genera of Psoraleae of the Succulent Biome affiliation and montane pantropical disjunction. The genus *Apios* has E Asia-E North American disjunction. Together the phaseoloids have 28 species in the flora with the ranges in E North America and belong to the Comanchian, E Prairie, E Madrean, Mesoamerican-Madrean, or Tamaulipan geoelements.

Thus, Papilionoideae I to IV have 45 species of 13 genera in the SC TX flora (57% of all papilionoids of the flora). All these genera with the exception of *Baptisia* and *Apios* have direct southern or Madro-Tethyan connections and are affiliated with succulent or grass/rainforest biomes of Schrire et al. (2005).

Remaining 18 species of the papilionoids are in the Hologalegina clade of Schrire et al. (2005). Among them are 4 species of non IRLC Hologalegina of the Succulent Biome affiliation with amphiatlantic and Tethyan disjunctions. The IRLC clade has 13 species of Galegeae, with 12 species being of the genus *Astragalus*. According to Scherson et al. (2008), *Astragalus* arrived from Asia via the Bering Strait. This genus is among the few legumes in SC TX flora which represent large north temperate, mostly Old World, radiation in the IRLC clade. The 13th species, *Lathyrus pusillus*, found throughout temperate South America and disjunctly in the south-central United States, is in the South American *Notolathyrus* clade. It was suggested that it originated by long-distance dispersal of taxa to South America from Eurasia (Kenicer et al. 2005). It is outside of the relatively recent transberingian clade of these authors' phylogeny which contains the eastern Eurasian species (ancestral stock) and the majority of extant North American *Lathyrus* species.

Thus, the overwhelming majority of the native legumes in the SC TX flora has direct connections with Madrean/Mesoamerican, Tethyan, or South American radiations. The Old World Tethyan genera (with the exception of *Astragalus*) as well as Southern Hemisphere genera present in the flora used the transatlantic crossing in most cases.

The Cyperaceae have 69 species of 11 genera and are in fourth place in the flora of SC TX. Because they occupy mostly wetland-aquatic habitats and have broad species ranges, they are not very informative biogeographically. However, unlike more temperate floras, e.g., flora Armenia (Saghatelyan 2006), the proportion of temperate and subtropical species of Cyperaceae in SC TX is significantly shifted towards tropical/subtropical/warm temperate ones. The largest genus of sedges in the flora is *Cyperus* (20 sp.) with *Carex* having only 14 species, while in more temperate latitudes *Carex* has more than a hundred species per flora of similar size. Genus *Eleocharis* (14 sp. in SC TX) has centers of diversity in the Amazon rainforest and adjacent eastern slopes of the South American Andes, eastern North America, California, Southern Africa, northern Australia, and subtropical Asia. A majority of species of Cyperaceae in SC TX flora has southeastern North American-Mesoamerican, E North American, and tropic/subtropical ranges. Five more Cyperaceae genera with 14 species in the flora also have tropical to warm temperate distribution.

Fifth place in the SC TX flora is occupied by Euphorbiaceae with 68 species in 12 genera. Subfamily Acalyphoideae has 4 genera and 21 species in the flora. *Argythamnia* and *Bernardia* are tropical/subtropical American genera extending to Sonoran-Chihuahuan Subprovinces in the southwestern United States. Three of their eight species in the flora are Edwards Plateau endemics. *Tragia* and *Acalypha* are broadly tropical/subtropical genera. Native to the Americas species of *Acalypha* (seven sp. total in the flora) comprise two-thirds of the genus and have mostly eastern and southern distribution in the United States. *Acalypha* is sister to the tropical West African genus *Mareya* and is nested among strictly Old World genera (Wurdack et al. 2005).

Subfamily Crotonoideae has two tropical/subtropical genera in the flora: *Jatropha*, with one Madrean and one Chihuahuan species, and *Croton*. Two thirds of all species of the genus *Croton* are restricted to the Americas while one third is scattered in the Old World (Van Ee et al. 2011). Six of the nine of its species in the flora have south-central North American ranges and belong to the two endemic North American/Mexican sections. The remaining three species are in the two Mexico/Mesoamerica/South American sections of Van Ee et al. (2011).

Half of the species of Euphorbiaceae of the flora belong to the largest subfamily Euphorbioideae with the majority of species in the *Euphorbia* subg. *Chamaesyce*. Subgenus *Chamaesyce* has the Old World origin and includes the largest New World radiation within the Old World-centered genus *Euphorbia* (Yang et al. 2012). The base of subgenus *Chamaesyce* consists of several clades distributed in Africa (Zimmermann et al. 2010). New World groups in the subg. *Chamaesyce* had more than one origin from the Old World group. The section *Crossadenia* became established in Brazil first, and later there was a separate introduction accounting for the rest of the New World clade which includes 500 species (Yang et al. 2012). The *Chamaesyce* clade of that subgenus, which originated in arid areas of North America diversified locally into three major clades: the Acuta clade with 3 endemics in southwestern U.S.A. and N Mexico, the Peplis clade, mostly endemic to southwestern U.S.A. and N Mexico, and Hypericifolia clade, which subsequently achieved worldwide distribution through multiple long-distance dispersal events (Yang & Berry 2011). There are 20 species of *Chamaesyce* in the SC TX flora from all three lineages with the ranges in various parts of warm temperate and subtropical North America.

According to Zimmerman et al. (2010), *Euphorbia* evolved from progenitors of the subgenus *Esula* in South Africa and had long distance dispersal from Africa to South America and farther to North America. All remaining species of *Euphorbia* in SC TX flora belong to that subgenus *Esula*, members of which are mostly herbaceous in the northern hemisphere. They fall in the *Euphorbia spathulata* (one sp.) group and *Euphorbia commutata* (6 sp.) group. *Euphorbia spathulata* is one of the most widespread native species of *Euphorbia* in the New World, occurring in most of North America. In the phylogeny of Zimmerman et al. (2010), the species are nested among Eurasian and Frontal Asian species, and a southwestern North American *E. alata*. The remaining six species of *Euphorbia* of the flora are annuals of the *Euphorbia commutata* group of the section *Peplus* (Geltman et al. 2011). It has diversified greatly from Western Asia to Europe and to North America and lacks true succulents (Bryuns et al. 2011). Besides *E. commutata* (E/NE North American), the group has a SC U.S.A., an Edwards Plateau, and an E Comanchian species in SC TX flora. The concentration of the American species of the subgenus *Esula* in the eastern and southeast-central North America coupled with wide Eurasian distribution of subgenus *Esula* resembles the Africa-Mediterranean/Eurasia- transatlantic crossing scenario for some legumes and Asteraceae mentioned earlier.

The genus *Stillingia* (two sp. in the flora) of the Euphorbioideae is paraphyletic in an almost exclusively Neotropical clade with three other genera (Wurdack et al. 2005).

An example involving vicariance events comes from the former Euphorbiaceae tribe Porantheread (family Phyllanthaceae by APG 2009). An endemic North American clade of *Andrachne* section *Phyllanthopsis* (Vorontsova et al. 2007) includes two species disjunctly distributed in Trans-Pecos-Coahuila, Edwards Plateau, and Ozarks Plateau. This clade is sister to the *Leptopus* + *Actephila* (Vorontsova et al. 2007) clade of mesophyllus shrubs. The latter clade is disjunctly distributed in the relictual humid forests of Euxinian and Hyrcanian Provinces of Takhtajan's Floristic System in Transcaucasia, in the Sino-Himalayan Province of Wu (1979), and Indonesia plus a clade of Asia and Australasia. This is a striking example of subtropical Northern Hemisphere (Madro-Tethyan) radiation along the northern Tethys shore that is sister to the tropical Africa/Madagascar-Australian radiation of the *Andrachne* s.s. clade. The latter clade is basally branching in the "clade A" of the Porantereae phylogeny of Vorontsova et al. (2007) and consists of xerophytes from the Horn of Africa. It started the first Madro-Tethyan (southern shore) radiation with two species in Mexico and Peru and a large xerophytic radiation in the Tethyan Subkingdom. Thus, there might have been two transatlantic migrations from North Africa and two single colonization events to North America, followed by vicariance events, and a single long-distance dispersal to Peru.

Cactaceae with 40 species of 13 genera is in sixth place in the flora. The broadly American Opuntioideae is represented by 13 species, while the remaining 27 species belong to the tribe Cacteae of Cactoideae. The species of Cacteae have mostly Chihuahuan-Tamaulipan ranges, while the Opuntioideae have a broader distribution in the North American southwest. The cacti originated in northern South America in mid-Tertiary; Opunioideae and Cactoideae occur mostly in South America while the tribe Cacteae is exclusively North American (Nyffeler 2002).

Middle sized families of SC TX flora, Brassicaceae (37 sp. /14 gen.) and Lamiaceae (36 sp. /11 gen.), are more numerous in the Tethyan floras of the Old World where they have their major centers of diversity. For example, flora Armenia has more than twice the number of species and a higher percentage of endemism in these families than those of either the SC TX or Big Bend (Saghatelyan 2006). *Salvia* (12 sp. in SC TX/19 sp. in Armenia) is the only large genus of mints in SC TX flora. The New World *Salvia* subgenus *Calosphace* (500 sp. total) has centers of diversity in Mexico and South America (Walker & Sytsma 2007). Mexico is supported as the geographic origin of *Calosphace* and dispersal events to South America account for its current disjunctive distributions (Jenks et al. 2012). The close affinity of a group of South African species of *Salvia* to the SW American species in *Salvia* sect. *Heterosphace* suggests a single dispersal from the Old World to the New World with subsequent diversification (Walker et al. 2004).

For Brassicaceae, the following numbers were published in Koch & C. Kiefer (2006): ca. 900 sp. in the Irano-Turanian region, ca. 630 sp. in the Mediterranean region, and ca. 778 sp. in North America. The family Brassicaceae is thought to have originated in the Irano-Turanian region, where the highest species diversity is found (Hedge 1976) and where *Aethionema,* the genus sister to the rest of the family, is also most diverse (Al-Shehbaz et al. 2006; Couvreur et al. 2010). In the flora Armenia it is the fourth largest family with 195 species (5.8% of all species of the flora), while Texas with the area 21 times larger than that of Armenia, has only 93 species (2% of the TX flora). The Bering Land Bridge is a probable route to North America from NE Asia since most of the diversity of the family in North America is concentrated in its western half. The Beringian crossing was suggested for *Lepidium* (Mummenhoff et al. 2001), *Draba* (Koch & Al-Shehbaz 2002), and for other Brassicaceae genera. The same Beringia crossing scenario is repeated for Tethyan groups from other families, like *Astragalus, Artemisia, Silene*, Boraginoideae, and Betoideae. However, these groups are absent or not diverse in the SC TX flora.

The Plantaginaceae has 34 species in 11 genera in SC TX flora. The discussion below is based upon the phylogenetic tree of Albach et al. (2005). The mainly south and Central American tribe Gratioleae has five species of three Neotropical genera in the flora: *Bacopa, Mecardonia,* and *Stemodia.* South American Angelonia clade is sister to the Gratioleae, and together these clades form the first major group of Plantaginaceae (Albach et al. 2005). Cheloneae also have a New World ancestry with the basal genera in Mesoamerica and only one Old World genus in Japan and eastern Russia (Wolfe 2002). North American members of Cheloneae diversified initially in the Klamath Region with subsequent migration to the Rocky Mountains (Wolfe et al. 2002). An endemic North American genus of this tribe *Penstemon* (271 sp. total, 10 sp. in the SC TX flora) originated in the Rocky Mountains, radiated throughout western states, and then to the south and east (Wolfe et al. 2006). A similar general pattern of north-to-south and west-to-east dispersal for two other genera of Cheloneae, *Collinsia* and *Tonella*, was found by Baldwin et al. (2011). Next tribe, mostly Old World Veroniceae (2 sp. in SC TX), was shown to be sister to *Plantago* (10 sp. in the flora) which is sister to the South American paramo genus *Aragoa* (Bello et al. 2002). Albach et al. (2005) suggested that an ancestor of *Aragoa* migrated from the Old World to the New World and later adapted to the high Andean paramo environment.

The biogeography of the next tribe Antirrhineae (three sp. of *Maurandella* and *Nuttallanthus* in SC TX) suggests its Old World origin with two subsequent dispersal events to the New World (Albach et al. 2005). Based on their phylogenetic hypothesis, Albach et al. (2005) infer a New World ancestry of the Old World clade because *Russelia, Tetranema,* and Cheloneae are sister to the rest of this clade, and together they are sister to the New World Gratioleae-Angelonia clade. The disjunction of Plantaginaceae taxa between the New World and Old World, especially the Mediterranean region, exemplifies the biogeographic pattern of Madro-Tethyan disjunction.

The Chihuahuan-Tamaulipan desert genus *Leucophyllum* (2 sp.) is the only genus of the reorganized Scrophulariaceae in the flora. *Leucophyllum* is in a clade with Myoporaceae and together they are sister to the mostly South American and E Asian Buddlejaceae (Olmstead et al. 2001). The temperate to tropical family Myoporaceae is mainly distributed in Australia, with a few representatives in South Africa, Eastern Asia, and West Indies (Watson & Dallwitz 1992).

Solanaceae has 28 species in 10 genera in the flora. Olmstead et al. (2008) suggested the New World as the most likely place of origin for Solanaceae. The SC TX flora has mostly large and broadly distributed genera, like *Solanum* (7 sp.) and *Physalis* (7 sp.) with the species ranges in western and SWC North America, the Sonoran and Madrean provinces. *Lycium*, which has a center of diversity in southwestern North America (Levin et al. 2011) has 5 species in the BB flora of the Madrean Region, but only one species in SC TX flora.

The cosmopolitan Pteridaceae (27 sp. in SC TX) has 24 species in common in the two Texas floras. In the SC TX flora more species of Pteridaceae have eastern N American ranges, while the BB flora has six more Madrean/Chihuahuan species.

The next family in the SC TX flora, mostly Laurasian temperate Rosaceae, has only 27 species (1.6%) in 10 genera. This is twice the number of Rosaceae in the BB flora, but only about one third of the Rosaceae in a typical mountainous temperate Eurasian flora. The flora of Armenia, for example, has 163 species of Rosaceae (4.9% of the flora). The bulk of the Rosaceae family in SC TX flora is comprised of largely distributed holarctical genera, like *Prunus* (9 sp.), *Crataegus* (7 sp.), *Rubus* (3 sp.), and *Rosa*. Most of these genera are of the Old World origin. There are also two species of western North American genera, *Fallugia* and *Petrophytum,* in both TX floras.

Apiaceae has 24 species in 18 genera in the SC TX flora. *Sanicula canadensis* is the only species of this widely distributed temperate genus in the flora. Southern African origins of subfamily Saniculoideae and of both of its tribes are supported by a DIVA analysis (Calvino et al. 2008a). The genus *Eryngium* has four species in the flora. The ancestor of *Eryngium* was inferred by Calvino et al. (2008b) to have occurred in the western Mediterranean, whereupon the genus split to the two major clades, the Old World clade and the New World clade. The basal lineages in the New World clade show semi-aquatic preferences, and one of them, *E. nasturtiifolium* of the “Eastern U.S.A. clade” of Calvino et al. (2008b), shows similarities with species from the western Mediterranean. One of the biogeographical scenarios proposed by the authors for the “Eastern U.S.A. clade” is that the dispersal from the western Mediterranean to the eastern U.S.A. or Mexico may have been by water. Another species of *Eryngium* in the flora, *E. yucciifolium*, is in the “North American Monocotyledonous clade” of these authors. For that clade a different scenario was proposed: it originated by dispersal from central-east South America (SE Brazil), a center of diversification which, in its turn, originated after a separate trans-Atlantic dispersal from Africa.

The rest of the Apiaceae species of the flora are in the African based subfamily Apioideae which is widely distributed in North temperate latitudes. In North America their ranges are mostly in eastern and south-eastern parts. In SC TX flora seven of these species are in the four genera of the tribe Oenantheae of the "North American Endemics clade." It is a sister group to a clade composed primarily of Old World taxa (Downie et al. 2008). Six more genera are in the "Selineae clade" (Downie et al. 2010). Apioideae originated in southern Africa and migrated north along two different tracks: the eastern and western. The radiation of euapioids occurred in Eurasia with the trans-Atlantic connection being as important as the trans-Pacific one. For both tracks, the prevailing direction of dispersal was from the Old World to the New World (Banasiak et al. 2013). The apioids found in SC TX flora, judging from their present distribution and connections, probably used the north temperate trans-Atlantic crossing.

Western hemisphere family Onagraceae has 24 species of three genera in the flora. There are four species of the genus *Ludwigia* of one of the three basally branching Neotropical clades. The remaining 20 species are in the tribe Onagreae which is endemic to southwestern North America (Katinas et al. 2004). The Big Bend flora has 12 species in common with the Onagreae of the SC TX flora.

The Malvaceae has 24 species in 12 genera. All these genera are in the tribe Malveae which centers in the Americas, but also contains South Pacific and European taxa (Tate et al. 2005). Half of these species belong to pantropical or warm temperate to tropical/subtropical genera, with the rest in the Mexico/Texas or North/South American genera. The Malveae of the flora have tropical/subtropical American connections.

SUMMARY OF TAXONOMIC GROUPS IN SC TX FLORA

Thus, taxonomic groups of SC TX flora exhibit several different patterns. The species of many woody genera like *Carya, Juglans, Platanus*, *Acer, Quercus, Rhus*, *Cornus, Diospyros, Viburnum*, and *Lonicera,* show tertiary Laurasian flora vicariance pattern. This genera are olygotypic or monotypic in the flora. Among the larger families mentioned in the discussion above, those with the Old World roots whose ancestors used transatlantic crossing are much more numerous than those whose ancestors came from Asia via Beringia. These numbers drop significantly for BB flora, exemplified by a four-fold decrease of the number of species of Apiaceae there. Long distance dispersals of these ancestral taxa were occurring from the Mediterranean to Mesoamerica/North America or from Africa to South America (SE Brazil) first, followed by dispersal to Mesoamerica/North America. Madro-Tethyan vicariance and/or bidirectional migrations were important in the assembly of the flora. Such examples are represented by *Ephedra*, *Juniperus,* Cesalpinioideae and some other legumes, Plantaginaceae, *Mahonia, Pistacia, Arbutus*, *Helianthemum,* and *Eryngium*. Western Hemisphere groups have south/north connections and are more mesophitic in SC TX than in BB, with the latter having higher numbers of xerophytes, like Cactaceae. The xerophitic groups tend to have more western (Andean) south/north connections. Cosmopolitan families, like Poaceae and Cyperaceae, have more tropical/subtropical representatives in the flora than temperate ones. Mesophyllous tropical groups are more numerous in SC TX than in BB flora. Southwestern North American centers of xerophytic speciation in many Asteraceae, the Chamaesyce clade, Cactaceae, Agavaceae, and others, as well as the Mexican centers in *Salvia, Quercus,* and many Madrean genera played an important role in the assembly of the SC TX flora.

MAJOR GENERA

The largest genera of the flora are listed in Table 2. First 40 genera of the spectrum include only 434 species (27% of the flora). The generic diversity is high, but there are no speciose genera, with the two largest ones having only 20 species each. Compared to the generic spectrum of BB flora, more-speciose in SC TX are four major Cyperaceae genera, as well as *Prunus, Tradescantia, Symphiotrichum,* and *Yucca*, while *Chamaesyce* and *Muhlenbergia* have more species in the BB flora.

Major geographical groups of widely distributed temperate genera in the SC TX (SC) and BB floras are as follows.

Broadly temperate Old World-New World genera are exemplified by *Salvia* (12/12), *Stachys* (1/1), *Artemisia* (1 E SC 5 BB), *Solidago* (7 SC 5 BB), as well as several genera of the Pooideae.

Table 2. Large and middle size genera of the SC TX flora.

Genus	No. of species in each genus
Chamaesyce, Cyperus	20
Dalea	18
Oenothera, Quercus	17
Juncus, Muhlenbergia	16
Bouteloua, Eleocharis	14
Carex	13
Salvia	12
Asclepias, Astragalus, Cheilanthes	11
Euphorbia, Erigeron, Panicum, Penstemon, Plantago, Symphiotrichum	10
Acacia, Aristida, Eragrostis, Physaria, Ruelia, Setaria, Sporobolus	9
Selaginella, Tradescantia, Yucca, Linum, Prunus	8
Desmanthus, Elymus, Galium, Opuntia, Polygala,	8
Mimosa, Solanum, Physalis	7
Echinocereus	6

North temperate Old World genera originated in the Tethyan Subkingdom and arrived to Western North American via Beringia: *Astragalus* (10 SC 11 BB), *Silene* (1 SC TX/2 BB), *Allium* (4 SC TX/6 BB), *Lithospermum* (4 SC 5 BB), and *Omphalodes* (1/1). Some other genera, like *Helianthemum* (1/1) and *Linum* (9 SC/8 BB) arrived to Eastern North America from Europe.

Cold temperate genera with major centers of diversity in Eastern Asia. In the United States this group has mostly radiated in the western mountainous part and has few species in Texas: *Arenaria* (1 SC TX/5 BB), *Anemone* (2 SC TX/3 BB), *Clematis* (2 SC 3 BB), *Delphinium* (2 SC 3 BB), *Draba* (3/3), and *Aquilegia* (2 SC 1 BB).

Widely and disjunctly distributed woody North temperate genera like *Cercis* (1/1), *Crataegus* (7 SC 1 BB), *Prunus* (9 SC 4 BB), *Lespedeza* (3 SC 1BB), and *Vitis* (6 SC 1 BB). For *Juglans* (3 SC 2 BB), *Fraxinus* (6 SC 4 BB), and *Acer* (2 SC 1 BB) a North American origin was proposed (Manchester 1999), while for *Lonicera* (1/1) and *Viburnum* (1 SC 2BB) an E Asian origin was proposed (Bell & Donoghue 2005).

Madro-Tethyan genera disjunctly distributed in the Tethyan and Madrean Subkingdoms: *Ephedra* (5 SC 4 BB), *Arbutus* (1/1), *Styrax* (1 SC 0), *Oligomeris* (1/1), *Maurandella* (1/1) and *Nuttallanthus* (2 SC 1 BB). There are two more genera of this group in BB, *Cupressus* and *Peganum,* absent from SC TX flora.

Comparison of the generic geographical spectra of the two floras reveals 132 different genera in the SC TX flora not found in the BB flora (Table 3). Of these 54 (41%) are broadly tropical/subtropical genera, 14 are E North American, eight are E Asia-E North American and eight are SC U.S.A. genera. The numbers of differential temperate Northern Hemisphere genera are comparable: 18 genera in SC TX and 17 in BB flora. The BB flora has total 100 differential genera 57 of which are West and SW North American genera, while 26 genera are mostly American tropical/subtropical. These numbers illustrate that SC TX has more tropical/subtropical connections, including connections to the floras in the Old World. The BB spectrum exhibits closer ties with western North American floras, has more species of the xeric genera of the Madrean Region and connections to the mostly Western Neotropics.

Woody genera have more species in the SC TX flora. For example, in SC TX *Crataegus* and *Prunus* each has 7 species; *Vitis* has 5 species, while in BB flora these genera have only one species each. In the SCTX flora higher species numbers in mesophyllous, including relictual, genera and more connections with the N American Atlantic Region are evident from the comparison of the generic spectra of the SC TX and BB floras. This comparison supports their position in different chorionomic regions of the North American flora.

GEOGRAPHIC ELEMENTS OF THE FLORA

Detailed descriptions of the geographic elements are given in Saghatelyan (2009). Below are brief descriptions and sample taxa for each geoelement. The geographic spectrum of the flora is illustrated by Tables 4 and 5. All phytochoria are assumed within the Takhtajan (1986) System boundaries.

Table 3. South-Central TX genera not found in Big Bend.

Tropic/Subtropical: 54 genera
Temperate N Hemisphere: 18 genera
Temperate/Subtropical/ (Tropical) Asia (E) - E N America: 8 genera
N American: 8 genera
E N American: 14 genera
SC US (TX): 8 genera
Sw US-N Mexico: 4 genera
Cosmopolitan: 8 genera

Table 4. Geographical spectrum of the SC TX (SC) flora and Big Bend (BB) flora. Numbers of species attributed to major geographic elements are in bold; numbers of species of the subelements are in regular typeface. The geoelements are listed by the higher chorionomic units in the systems of Takhtajan (1986) and McLaughlin (2007). Their grouping is somewhat modified based on the present data.

Geoelement	SC	BB	
Of Broad Distribution—143 spp. (9% of flora)			
Polichorous	26 / 1.6	14 / 0.8	
Holarctical	13 / .8	21/ 1.3	
Tropical/Subtropical	30 / 1.8	32 / 2.0	
American wide	74 / 4.5	101 / 6.3	
Holarctic Subkingdom/N American Atlantic Region—794 spp. (49% of the flora)			
North American	149 / 9.2	98 / 6.2	
E North American / SE North American	236 / 14.6	37 / 2.3	
Gulf Coast	17 / 1.0	--	
Prairie	159 / 9.8	85 / 5.4	
Comanchian	63 / 3.9	46 / 2.9	
SC USA/SC North American	63 / 4.0	0	
Tamaulipan	34 / 2.0	5 / 0.3	
Edwards Plateau	71/ 4.3	0	
Madrean Subkingdom/Western N America—450 spp. (28% of the flora)			
W North American	58 / 3.6	114 / 7.2	
SW North American	35 / 2.2	149 / 9.4	
SWC North American	47 / 2.8	0	
Amphitropical	10 / .6	19 / 1.2	
Sonoran	35 / 2.2	82 / 5.2	
Chihuahuan	194 /12.0	253 / 16.0	
Including Chihuahuan-Tamaulipan	66	45	
Including Sonoran-Chihuahuan	18	80	
South Texas /Coahuila Endemic	72 / 4.4	103 / 6.5	
Including SC TX/SE TX Endemic	35	--	
Including South TX/SEC TX /Coahuila	37	--	
Madrean Subkingdom/Neotropical Kingdom—212 spp. (14 % of the flora)			
Madrean		101 / 6.2	192 / 12.1
Including E Madrean	35	--	
Mesoamerican	49 / 3.0	84 / 5.3	
Caribbean	11 / 0.7	--	
American Tropical/Subtropical	52 / 3.2	--	
Not Established	18 / 1.1	25 / 1.6	

Polichorus: wide distribution on several continents; 26 species. These are wetland, aquatic, and weedy species of cosmopolitan herbaceous genera.

Holarctic: wide ranges in north temperate latitudes of the New and Old World; 13 species. These are hydrophytes (*Nuphar lutea*) and mesophytes (*Sambucus nigra*).

Tropical/Subtropical: wide distribution in tropical and subtropical latitudes; 30 species. Among them are 8 species of grasses and 7 species of Cyperaceae. **Trop/Subtr/Warm Temperate subelement:** mostly in subtropical and warm temperate regions (*Malvaviscus arboreus*) or extending from tropical to warm temperate latitudes (*Cyperus flavescens*).

American Tropical/Subtropical: 52 species. These are American species of genera of different origin. Some of them are species of Mexican genera extending to southern United States or of tropical Central and northern South American genera, like *Agave*. Others are species of broadly tropical American genera, like *Baccaris* and *Tillandsia*, tropical/subtropical genera, like *Acacia* and *Boerhavia*, or cosmopolitan genera, like *Eleocharis*. The Poaceae (15 sp.) and Cyperaceae (7 sp.) are important in this group.

American: wide distribution in the Americas; 74 species. Many of them grow in different types of habitats (*Plantago patagonica*) or are hydrophytes (*Lemna minuta, Najas guadalupensis*). Species of different families are in this group with many in Poaceae (16 sp.) and Asteraceae (6 sp.).

North American: wide ranges in temperate regions of North America; 149 species (9% of the flora). Many hydrophytic and mesophytic species of cosmopolitan genera are in this group. They are mostly grasses (30 sp.), Asteraceae (15 sp.), sedges and rashes (11 sp. each).

East North American: wide ranges in the Atlantic North American Region; 236 species (17% of the flora). Among them are 52 species of **SE North American subelement** with more narrow southern ranges. This geoelement includes 60 mesophyllous woody species, like relictual Laurasian *Platanus occidentalis, Juglans nigra,* and *Hamamelis virginiana*. The SE North American subelement is exemplified by *Taxodium distichum, Sabal minor,* and *Smilax bona-nox*. Other prominent groups in this geoelement are grasses (34 sp.), Asteraceae (32 sp.), Cyperaceae (15 sp.), Fabaceae (11 sp.), and Apiaceae (10 sp.). Connections across the Atlantic are prevalent in many relictual amphiatlantically disjunct genera of this geoelement, for example, in *Cercis* and *Gleditsia*. The species of East Asia-E North American disjunctive genera, like *Lespedeza*, are also in this group as are representatives of tropical genera, like *Bignonia, Diospyros,* and *Passiflora*.

Gulf Coast: ranges in the Atlantic and Gulf Coastal Plain Province; 17 species. Some of them are in genera with amphi Atlantic disjunctions, like *Linum, Quercus,* and *Sesbania*, while others are in genera with pantropical disjunctions (*Zornia, Tridens*).

Prairie: wide ranges in the North American Prairies Province; 159 species (9% of the flora). All but 7 species of this geoelement are herbaceous with the Asteraceae being most diverse (38 sp.), followed by the grasses (18 sp.) and legumes (15 sp.). Among the Asteraceae the Astereae (14 sp.) and Heliantheae (9 sp.) are important, while eight other clades have no more than one to three species in this geoelement. Half of the prairie grasses are in the tropical to warm temperate subfamily Chloridoideae. Connections across the Atlantic (in *Linum, Mimosa*, *Rhynchosia,* and *Erythronium*) and pantropical disjunction (in *Desmodium*) are important. The New World genera, like *Sisyrynchium* and *Triodanis*, SW North American genera, like *Dalea*, and W North American genera, like *Penstemon*, each have several species in this geoelement.

Comanchian: ranges on the Edwards Plateau extending northward into central Oklahoma/Ozark Plateau, southward into northeastern Mexico and western Louisiana; 63 species. Asteraceae (15 sp.), Fabaceae (12 sp.), and Apiaceae (7 sp.) are important in this geoelement. Rosaceae, Lamiaceae and Agavoideae have 4 species each. Tropical/subtropical genera, like *Eryngium* and *Zanthoxylum*, SW North American genera, like *Gutierrezia* and *Yucca*, are well represented, while grasses only have two species of Chloridoideae in this geoelement.

SC USA/SC North American: from Central and South Texas extending northward to adjacent states and southward to northern Mexican Plateau; 63 species. Among them are Asteraceae (11 sp.), Poaceae (10 sp.), and Euphorbiaceae (6 sp.); remaining genera are from different families and have just 1–2 species each (*Plantago, Lechea, Phlox, Linum,* and *Salvia*).

Tamaulipan: from south-eastern and south-central Texas to Tamaulipas in Mexico; 34 species. The majority of them are in tropical/subtropical (*Ehretia, Sesbania, Condalia*) or tropical to warm temperate (*Cynanchum*) genera. A few species are in north temperate (*Crataegus*) and amphitropical (*Krameria*) genera. All these genera except *Condalia* (2 sp.) are monotypic in the flora.

W North American: wide ranging in western North America mostly north of Mexico or in its parts; 58 species. These species belong to mostly cosmopolitan (*Chenopodium*), largely Holarctic (*Corydalis, Draba*), North American (*Helianthus*), or tropical to warm temperate (*Rhus*) genera. Asteraceae with 12 species is the largest family of this geoelement.

SW North American/SW USA: embraces southern part of the Rocky Mountain Province, Colorado Plateau, southern and eastern Great Basin, and the Sonoran Province eastward through New Mexico to southwestern Texas and southward to adjacent northern Mexico; 35 species. These are species of W North American genera (*Fendlera, Sphaeralcea*), broadly North American genera of western origin (*Penstemon*), or tropic/subtropical American genera (*Mentzelia*). The largest families in this geoelement are Asteraceae (7 sp.) and Cactaceae (6 sp.).

SWC North American /SWC USA: more eastern than the previous geoelement including western part of the Prairie Province; 471 species. These are species of W North American (*Nama, Phacelia*) genera, American-African (*Asclepias, Pomaria, Mimosa*), tropical (*Senna*), tropical American (*Bouteloua*), and North American (*Monarda*) genera.

Amphitropical: disjunctive ranges in warm temperate deserts of the western North and South America; 10 species of peculiar desert genera, like *Koeberlinia, Aloysia,* and *Kallstroemia*.

Madrean: ranges embracing the Madrean Region, or mostly the mountains of Mexico; 101 species. This group has 21 species of woody genera (*Quercus, Acer,* and *Rhus*), 17 species of Asteraceae, 11 species each of the legumes (*Calliandra*) and ferns (*Notholaena*), 10 species of grasses, 6 of Euphorbiaceae (*Jatropa*), 6 species of Oleaceae (*Fraxinus*), and 3 species of gymnosperms (*Ephedra* and *Pinus*). The Madrean element has different subelements, North, South, West, and East. The largest, **East Madrean subelement** has 35 species: mostly in the Sierra Madre Oriental Province as defined by Morrone et al. (1999) extending northward to the Edwards Plateau and mountains in Trans-Pecos (*Quercus laceyi*).

Mesoamerican: wide ranges in Mesoamerica and the Caribbean Region extending to southern United States and northern South America–49 species. Many of them are in pantropical (*Cissus, Indigofera*) or tropical to temperate (*Ruellia, Cynanchum, Ipomoea*) genera; some, like *Eustoma*, are in Mega Mexico III genera (Saghatelyan 2009), or American-African genera (*Sideroxylon* and *Lantana*). There are also species of the Madro-Tethyan genera (*Arbutus* and *Pistacia*), as well as temperate to subtropical American genera (*Oenothera*). The largest in the Mesoamerican geoelement family Asteraceae has only 9 species, followed by Poaceae (5 sp.) and Cyperaceae (4 sp.). **Caribbean subelement** is extending to SE North America and has 23 species of different tropical/subtropical genera including six genera of grasses.

Sonoran: embracing mostly the Sonoran Sub-province or the entire Sonoran Province; 36 species. These are xerophytes from different families, the largest being Fabaceae (5 sp.) and Cactaceae (3 sp.). Eleven of these species are woody (*Mahonia trifoliata, Chilopsis linearis, Quercus grisea*).

Chihuahuan: ranges in the Chihuahuan Sub-province including Trans-Pecos and Edwards Plateau; 194 species. There are 38 species of Asteraceae, 18 of cacti, 19 of legumes, 12 of grasses, 10 of Euphorbiaceae, 8 species each of Solanaceae and Boraginaceae (mostly in tropical tribes, *Heliotropium* and *Tiquilia*), 5 species of Acanthaceae, 4 each of Brassicaceae, Agavaceae, Nyctaginaceae, and Lamiaceae. **Sonoran-Chihuahuan subelement** has ranges in the Sonoran and Chihuahuan Subprovinces; 21 species (*Lycium berlandieri, Cheilanthes villosa*). **Chihuahuan-Tamaulipan subelement** has ranges in the Chihuahuan Subprovince extending eastward to the Tamaulipan Subprovince; 66 species (*Matelea reticulata, Acacia rigidula, Dasylirion texanum*).

South Texas Endemic: 72 species. This element includes 35 species of **SC Texas/SEC Texas Endemic** and 37 species of **South Texas-Coahuila subelements.** SC Texas Endemic subelement is mainly found on Edwards Plateau extending to Trans-Pecos and along the Rio Grande valley to N Tamaulipan Subprovince. This element is closest to the Chihuahuan or Tamaulipan geoelement with narrow ranges in different parts of South Texas or SW Texas-Edwards Plateau, and Coahuila/Nuevo-Leon of northern Mexico. The species are from different xerophytic genera of different families and mostly have southern connections (*Opuntia edwardsii, Hesperaloe funifera, Menodora heterophylla*).

Edwards Plateau (Endemic): 71 species endemic or sub endemic to the Edwards Plateau. They are from different families, mostly Asteraceae (10 sp.), Fabaceae (6 sp.), Poaceae (4 sp.), and Euphorbiaceae (4 sp.).

The proportions of different geographical elements in the two TX floras are presented in Table 4. In the SC TX flora the largest geoelement, E North American, has 236 species, which, combined with 63 Comanchian, 64 SC USA, 33 Tamaulipan, 159 Prairie, 17 Gulf Coast species, 35 SC/SE Texas endemics, and 73 Edwards Plateau endemics, make 680 species or 42% of the flora. They belong to the N American Atlantic Region of North America. This group only has 11% in the Big Bend flora. The Chihuahuan element has 194 species (12%) in SC TX, but more species, 253 (16%), in Big Bend. There are only 101 species (6.2%) of the Madrean element in SC TX which has twice as much species in Big Bend (12.1%). The entire Madrean Region including the Sonoran, Chihuahuan, and Tamaulipan subprovinces, has 457 species (28%) in SC TX and 798 species (50%) in BB. The combined tropical element has 142 species (8%) in Big Bend and 142 (8.7%) in SC TX. Thus, the two floras are comparable in their southern connections, both having almost the same weight of tropical species. The influence of the Madrean Region is significantly stronger in the Big Bend flora, which has two times more Madrean and Sonoran species, while SC TX has more gulf coastal and SC North American species than BB. Thus, these two Texas floras, though in proximity to each other, represent two different chorionomic units: the N American Atlantic Region (SC TX), and Madrean Region (BB) of the North American flora.

CONCLUSIONS

There are 1619 native species of 626 genera and 149 families in the SC TX flora. Half of the 232 species of the largest family Asteraceae represent local diversification in the largest North American Heliantheae Alliance. Together with the taxa of several other clades of the family found in the flora they are mostly native to southeastern/southwestern/southern North America or have Central/South American connections. The ancestors of the basally branching taxa of many of these clades had either Mediterranean to Mesoamerica to North America or Africa to South America to North America long distance dispersals. Second largest family Poaceae (199 sp.) has 67% of its species in the tropical to warm temperate subfamilies. A majority (73%) of all the Fabaceae (120 sp.) have connections with SE N American/Madrean/Mesoamerican, Tethyan, or South American radiations. Old World Tethyan, as well as Southern Hemisphere legume genera found in the flora in most cases used the transatlantic crossing. The Cyperaceae (69 sp.), unlike those in more temperate floras, have a majority of species in tropical/subtropical/to warm temperate genera. Half of the Euphorbiaceae (68 sp.) species are in the Euphorbioideae, mostly in the *Euphorbia* subgenus *Chamaesyce,* which originated in arid North America after an introduction from the Old World. The species of Acalyphoideae and Crotonoideae comprise the other half the family and are in tropical/subtropical, mostly American genera. The middle sized families Brassicaceae (37 sp.) and Lamiaceae (35 sp.), with the only large genus *Salvia* are more prominent in the Old World Tethyan floras, where their major centers of diversity lie. To the contrary, the species of Plantaginaceae (34 sp.) belong to the mainly South and Central American clades with the basal genera in Mesoamerica and a pattern of Madro-Tethyan disjunction. The largest genera of the flora are *Chamaesyce, Cyperus, Dalea, Oenothera, Quercus, Juncus, Muhlenbergia, Bouteloua, Eleocharys, Carex,* and *Salvia*. There are 132 differential genera in the SC TX flora not found in the Big Bend flora. These include 54 tropic/subtropic genera, 34 temperate Northern Hemisphere, 14 E North American, 12 SC/SW USA-N Mexico, and 8 cosmopolitan genera. In the geographical spectrum of the SC TX flora the largest geoelement is comprised of 236 E North American species, which, combined with Comanchian, Tamaulipan, prairie, SC USA, gulf coast species, and local endemics, make 680 species (42% of the flora) of the North American Atlantic Region. This group only has 11% in the Big Bend flora. The Holarctic Subkingdom in general is represented by 793 species (49% of the flora). The Madrean Subkingdom/Western N America have 449 species (28% of the flora), followed by the Madrean Region/Neotropical Kingdom with 212 species (14% of the flora).

In general, in the SC TX flora the southern and eastern connections prevail. Transatlantic crossings, as well as S/N American bidirectional migrations were most important in the history of its assembly. This study supports placement of the SC TX flora in the N American Prairies Province of the N American Atlantic Floristic Region. In the McLaughlin (2007) classification it is a part of the Comanhian province. However results of this study support placement of the Comanchian chorion, including the SC TX flora, in the Atlantic Region rather the South Western Region of McLaughlin. The BB flora, which is just west of the continental divide from the SC TX flora, has a placement in a different region, namely the Chihuahuan Province of the Madrean Region.

APPENDIX 1

Checklist and area diagnoses of the flora of SC Texas. The following list of species was extracted mostly from the Synthesis of the North American Flora (Kartesz 2013) and it follows, with few exceptions, all the nomenclatural combinations as well as author citations of this source. The families of vascular plants are arranged in alphabetical order as are genera and species. Numbers by each family name indicate species/genera ratios in the family. The ranges of some species could not be referred to a particular geoelement. These are noted with a question mark in the checklist and are omitted from the analysis.

Abbreviations:

adv els—adventive elsewhere
Afr—African
Amphitrop—Amphitropical
Amer—American
Apach—Apachian
AZ—Arizona
Carib—Caribbean
C—central
Chih—Chihuahuan
Coah—Coahuila
CO—Colorado
Comanch—Comanchian
disj—disjunctive
E—East
Edw Plat—Edwards Plateau
FL—Florida
Gulf—Atlantic & Gulf Coastal Plain
intr els—introduced elsewhere
Madr—Madrean
Mesoam—Mesoamerican
Mont—montane
N—North
NM—New Mexico
OK—Oklahoma
Polichor—polichorous
Prair—Prairie
Roc Mt—Rocky Mountains Province
S—South
SC—south-central
Son—Sonoran Province
Tam—Tamaulipan Province
Temp—temperate
Trop/Subtr—tropical/subtropical
TX—Texas
USA—United States of America
W—West
WO—Wyoming

Counties: Bandera, Concho, Crockett, Edwards, Gillespie, Irion, Kendall, Kerr, Kimble, Kinney, Llano, Mason, Medina, Menard, Reagan, Real, Schleicher, Sutton, Tom Green, Uvalde, and Val Verde.

ANEMIACEAE 1/1

Anemia mexicana Mesoam

ACANTHACAE 7/19

Anisacanthus quadrifidus Chih
Carlowrightia texana Chih
Carlowrightia torreyana SC TX-Coah
Dicliptera brachiata E N Amer
Dyschoriste linearis SC USA
Justicia americana E N Amer
Justicia pilosella Chih-Tam
Justicia warnockii S TX-Coah (SW TX)
Justicia wrightii S TX
Ruellia caroliniensis E N Amer
Ruellia corzoi Chih
Ruellia drummondiana Edw Plat
Ruellia humilis E N Amer (+ Prair)
Ruellia metziae Edw Plat
Ruellia nudiflora Mesoam-Madr
Ruellia occidentalis E Madr
Ruellia parryi Chih
Ruellia yucatana Tam
Yeatesia platystegia Tam

ACERACEAE 1/2

Acer grandidentatum N Madr Mont
Acer negundo N Amer

AGAVACEAE 6/15

Agave lechuguilla Chih
Camassia scilloides E N Amer
Echeandia flavescens Son (W)
Hesperaloe funifera SC TX-Coah
Hesperaloe parviflora Comanch
Nolina lindheimeriana Edw Plat
Nolina texana SWC USA
Yucca arkansana Comanch
Yucca constricta SC TX (Edw Plat)
Yucca glauca Prair
Yucca pallida Comanch (S)
Yucca reverchonii Edw Plat (W)
Yucca rupicola Comanch (S)
Yucca torreyi Chih
Yucca treculeana Chih-Tam

AIZOACEAE 1/1

Sesuvium verrucosum Amer

ALISMATACEAE 2/5

Echinodorus berteroi Amer
Sagittaria brevirostra N Amer (N-C)
Sagittaria calycina N Amer
Sagittaria longiloba N Amer (W)
Sagittaria platyphylla N Amer (E)

AMARYLIDACEAE 3/7

Allium canadense E N Amer
Allium drummondii SC USA (Prair)
Allium kunthii Madr
Allium perdulce Prair
Cooperia chlorosolen SC USA
Cooperia pedunculata SEC USA
Nothoscordum bivalve E N Amer (+ Mesoam)

AMARANTHACEAE 9/17

Alternanthera caracasana Amer Trop/Subtr
Amaranthus albus Polichor
Amaranthus arenicola Prair wide
Amaranthus crassipes Carib
Amaranthus palmeri N Amer
Amaranthus polygonoides Carib
Amaranthus scleropoides Chih-Tam
Amaranthus tuberculatus N Amer
Celosia nitida Amer Subtr
Froelichia floridana N Amer (Prair-SE)

Froelichia gracilis N Amer
Gomphrena haageana S TX-Coah?
Gossypianthus lanuginosus N Amer (SC + Carib)
Guilleminea densa Madr
Iresine heterophylla Son wide
Iresine rhizomatosa E N Amer
Tidestromia lanuginosa SC USA

ANACARDIACEAE 3/7
Cotinus obovatus E N Amer disj
Pistacia mexicana Mesoam-E Madr
Rhus copallinum E N Amer
Rhus lanceolata SC N Amer
Rhus microphylla Son-Chih
Rhus trilobata W N Amer (+ W Prair)
Rhus virens Madr (E)

APIACEAE 19/25
Ammoselinum butleri E N Amer
Ammoselinum popei S Prair
Berula erecta Holarctical
Bifora americana Comanch (E N Amer)
Bowlesia incana Amer (Warm Temp)
Centella erecta SE N Amer (+ Mesoam-Carib)
Chaerophyllum tainturieri E N Amer
Cicuta maculata N Amer
Cymopterus macrorhizus Comanch (NC TX)
Daucosma laciniata ?
Daucus pusillus N Amer
Eryngium diffusum Comanch
Eryngium leavenworthii Comanch
Eryngium nasturtiifolium Madr (Mesoam-Madr)
Eryngium yuccifolium E N Amer
Eurytaenia texana SC USA
Hydrocotyle prolifera N Amer
Hydrocotyle umbellata Amer
Limnosciadium pinnatum SEC N Amer (Comanch?)
Polytaenia nuttallii Prair
Polytaenia texana Edw Plat?
Ptilimnium nuttallii SEC N Amer
Sanicula canadensis E N Amer
Spermolepis echinata N Amer (S)
Spermolepis inermis Prair

APOCYNACEAE 3/4
Amsonia ciliata SE N Amer (+ Comanch)
Amsonia longiflora Chih
Apocynum cannabinum N Amer
Telosiphonia macrosiphon S TX-Coah

AQUIFOLIACEAE 1/2
Ilex decidua E N Amer
Ilex vomitoria SE N Amer

ARACEAE 1/1
Arisaema dracontium E N Amer

ARECACEAE 1/1
Sabal minor SE N Amer

ARISTOLOCHIACEAE 2/3
Aristolochia coryi S TX Endemic
Aristolochia serpentaria E N Amer
Isotrema tomentosum E Prair-E N Amer

ASCLEPIADACEAE 4/21
Asclepias asperula SWC N Amer
Asclepias emoryi Tam
Asclepias engelmanniana SWC N Amer
Asclepias incarnata E N Amer
Asclepias latifolia SWC N Amer
Asclepias oenotheroides Mesoam (+ SC USA)
Asclepias texana S TX-Coah
Asclepias tuberosa N Amer (E + SW)
Asclepias verticillata E N Amer
Asclepias viridiflora E N Amer
Asclepias viridis SE N Amer (+ Prair)
Cynanchum barbigerum Tam
Cynanchum maccartii Edw Plat-Tam
Cynanchum racemosum Mesoam-Madr
Funastrum crispum SWC USA
Funastrum cynanchoides Madr (N & W)
Matelea biflora Comanch (W)
Matelea edwardensis Edw Plat
Matelea gonocarpos E N Amer
Matelea reticulata Chih-Tam
Matelea sagittifolia S TX Endemic

ASPARAGACEAE 1/1
Dasylirion texanum Chih-Tam

ASPLENIACEAE 1/1
Asplenium resiliens N Amer

ASTERACEAE 98/232
Achillea millefolium Holarctical
Acourtia nana Son-Chih
Acourtia runcinata Chih-Tam
Acourtia wrightii Son-Chih
Ageratina altissima E N Amer
Ageratina havanensis E Madr (+ Carib)
Amblyolepis setigera Chih-Tam
Ambrosia artemisiifolia Amer (mostly E)
Ambrosia confertiflora SWC N Amer
Ambrosia monogyra Son-Chih
Ambrosia psilostachya N Amer wide (Polichor)
Ambrosia trifida N Amer (mostly E)
Amphiachyris amoena Comanch (C/NC TX Endemic)
Amphiachyris dracunculoides Prair
Aphanostephus ramosissimus Chih-Tam
Aphanostephus riddellii Chih
Aphanostephus skirrhobasis SC N Amer
Arnoglossum plantagineum E Prair
Artemisia ludoviciana N Amer
Astranthium ciliatum Prair (SE)
Baccharis neglecta Chih-Tam
Baccharis salicifolia Amer Trop/Subtr
Baccharis salicina SW N Amer
Baccharis texana Prair (S)
Bahia absinthifolia Son-Chih
Baileya multiradiata Madr
Berlandiera lyrata Madr
Bidens bipinnata E N Amer-E Asian
Brickellia cylindracea Edw Plat
Brickellia dentata Edw Plat (+ E TX)
Brickellia eupatorioides N Amer
Brickellia laciniata Chih wide
Chaetopappa bellidifolia Edw Plat Endemic
Chaetopappa bellioides Chih-Tam
Chaetopappa effusa Edw Plat Endemic
Chaetopappa ericoides SW N Amer
Chaetopappa parryi Chihun-Tam
Chaptalia texana E Madr
Chloracantha spinosa Mesoam-Madr
Chromolaena bigelovii Chih?

Chrysactinia mexicana E Madr Mont
Cirsium engelmannii Comanch?
Cirsium horridulum E N Amer (Gulf-Mesoam)
Cirsium ochrocentrum W N Amer
Cirsium texanum Comanch
Cirsium turneri S TX-Coah Endemic
Cirsium undulatum WC N Amer
Conoclinium betonicifolium Gulf-E Madr
Conoclinium coelestinum E N Amer
Conoclinium dissectum Chih
Conyza canadensis Amer
Conyza ramosissima Prair (mostly N)
Coreopsis basalis SC USA
Coreopsis tinctoria N Amer
Croptilon divaricatum Gulf
Croptilon hookerianum Prair
Diaperia candida SC N Amer
Diaperia prolifera Prair (W)
Diaperia verna var. *verna* SW N Amer
Dichaetophora campestris SC TX
Dracopis amplexicaulis SE N Amer
Dysodiopsis tagetoides Comanch
Echinacea angustifolia Prair
Eclipta prostrata Amer with radiations
Engelmannia peristenia S Prair
Erigeron annuus E N Amer, adv els
Erigeron flagellaris W N Amer Mont
Erigeron geiseri Comanch
Erigeron modestus SWC USA?
Erigeron philadelphicus N Amer, adv els
Erigeron procumbens Gulf
Erigeron strigosus N Amer, adv els
Erigeron tenuis SE Prair
Erigeron tracyi SW N Amer
Erigeron versicolor?
Eupatorium serotinum E N Amer
Flaveria trinervia Mesoam-Madr with radiations
Florestina tripteris Chih-Tam
Flourensia cernua Son-Chih
Flyriella parryi Chih (ES)
Gaillardia aestivalis E N Amer (Prair-SE N Amer)
Gaillardia coahuilensis SC TX-Coah
Gaillardia pinnatifida SW N Amer
Gaillardia pulchella N Amer (mostly S-C)
Gaillardia suavis S Prair
Gamochaeta purpurea E N Amer, adv els
Grindelia adenodonta NCE TX endemic
Grindelia ciliata Prair
Grindelia grandiflora Chih-Tam
Grindelia havardii N Chih
Grindelia lanceolata Prair (E)
Grindelia pusilla S TX-Coah
Grindelia squarrosa Prair-W N Amer
Gutierrezia microcephala Madr
Gutierrezia sarothrae W N Amer
Gutierrezia sphaerocephala Chih-Tam
Gutierrezia texana SC N Amer
Gymnosperma glutinosum Mesoam
Haploesthes greggii SW Prair-Chih
Helenium amarum SE N Amer
Helenium autumnale N Amer
Helenium elegans SC N Amer
Helenium microcephalum SWC N Amer
Helianthus annuus N Amer-Polichor
Helianthus ciliaris SC N Amer
Helianthus grosseserratus Prair (N)
Helianthus hirsutus E N Amer wide
Helianthus maximiliani Prair
Helianthus petiolaris W N Amer
Heterotheca canescens Prair (SC-SW)
Heterotheca fulcrata W N Amer Mont
Heterotheca stenophylla Prair
Heterotheca subaxillaris N Amer
Hymenopappus artemisiifolius SC USA (E TX-W LA)
Hymenopappus flavescens SW N Amer
Hymenopappus scabiosaeus Prair
Hymenopappus tenuifolius Prair
Hymenoxys odorata SW N Amer
Isocoma coronopifolia Tam
Isocoma pluriflora Chih
Iva angustifolia ?
Iva annua Prair (E + E N Amer)
Krigia caespitosa E Prair (+ E N Amer)
Krigia occidentalis E Prair
Krigia virginica E N Amer wide
Lactuca canadensis E N Amer
Lactuca floridana E N Amer
Lactuca ludoviciana Prair
Laennecia coulteri N Madr
Liatris punctata Prair
Lindheimera texana Comanch
Lygodesmia texana S Prair-Chih
Machaeranthera tanacetifolia W N Amer
Marshallia caespitosa S Prair (Comanch)
Melampodium cinereum Chih-Tam
Melampodium leucanthum SWC USA
Mikania scandens E N Amer
Neonesomia palmeri SE TX-Tam
Packera obovata E N Amer
Packera plattensis EC Prair
Packera tampicana SC USA-Gulf
Packera texensis Edw Plat endemic
Palafoxia callosa Comanch
Palafoxia rosea Prair
Palafoxia texana Tam
Parthenium confertum Chih-Tam
Parthenium incanum Madr wide
Pectis angustifolia SWC N Amer
Perityle angustifolia SWC TX endemic
Perityle lindheimeri Edw Plat
Perityle warnockii SWC TX endemic
Pinaropappus roseus Madr-Mesoam
Plectocephalus americanus SC N Amer
Pluchea camphorata E N Amer
Pluchea odorata Amer (Mesoam-Warm)
Porophyllum scoparium Chih wide
Prenanthes carrii Edw Plat
Pseudognaphalium canescens W N Amer
Pseudognaphalium obtusifolium E N Amer
Pseudognaphalium pringlei Son-Chih
Pseudognaphalium stramineum W N Amer
Pseudognaphalium viscosum Mesoam
Psilostrophe gnaphalioides Chih-Tam
Psilostrophe villosa SW Prair
Pyrrhopappus grandiflorus S Prair
Pyrrhopappus pauciflorus S Prair ?
Ratibida columnifera Prair wide
Ratibida peduncularis Gulf-Tam

Ratibida tagetes SWC USA
Rudbeckia hirta E N Amer
Sanvitalia ocymoides N Chih-Tam
Senecio ampullaceus Comanch (E TX)
Senecio flaccidus Madr wide
Senecio riddellii W Prair
Shinnersia rivularis S TX-Coah
Silphium albiflorum Comanch (NCE TX endemic)
Silphium asteriscus E N Amer
Silphium integrifolium E Prair
Silphium laciniatum E Prair
Silphium radula E Prair
Simsia calva Chih-Tam
Smallanthus uvedalius E N Amer
Solidago altissima E N Amer
Solidago gigantea N Amer
Solidago juliae Chih
Solidago nemoralis E N Amer
Solidago odora E N Amer (Gulf)
Solidago petiolaris E N Amer
Solidago radula E Prair-(Carolinian)
Stephanomeria pauciflora W N Amer
Symphyotrichum drummondii E Prair
Symphyotrichum ericoides N Amer
Symphyotrichum lanceolatum N Amer
Symphyotrichum oblongifolium Prair
Symphyotrichum patens E N Amer
Symphyotrichum praealtum Prair wide
Symphyotrichum pratense SE Prair
Symphyotrichum sericeum E Prair
Symphyotrichum subulatum Amer (coastal)
Tetragonotheca texana Chih-Tam
Tetraneuris acaulis WC N Amer
Tetraneuris linearifolia SC N Amer
Tetraneuris scaposa SWC N Amer
Thelesperma ambiguum Tam
Thelesperma filifolium Prair
Thelesperma longipes Chih (+ S AZ)
Thelesperma megapotamicum Prair
Thelesperma simplicifolium Chih-Tam
Thymophylla acerosa N Madr wide
Thymophylla micropoides Chih
Thymophylla pentachaeta Madr
Thymophylla setifolia Chih
Thymophylla tenuiloba Tam, adv els
Verbesina encelioides Amer
Verbesina lindheimeri Edw Plat
Verbesina nana SW TX-Coah
Verbesina virginica E N Amer
Vernonia baldwinii Prair (C-E)
Vernonia ×guadalupensis Edw Plat
Vernonia lindheimeri SC TX-Coahuila
Vernonia marginata W Prair-Chih
Viguiera dentata Mesoam-Madr
Viguiera stenoloba Madr (Chih wide)
Wedelia acapulcensis Mesoam-Madr
Xanthisma spinulosum W N Amer
Xanthisma texanum SC USA
Xanthium strumarium Amer, adv. els
Zinnia anomala Chih
Zinnia grandiflora S Roc Mt-Son

AZOLLACEAE 1/1
Azolla caroliniana E N Amer

BERBERIDACEAE 1/2
Mahonia swaseyi Edw Plat (C TX endemic)
Mahonia trifoliolata Son

BIGNONIACEAE 3/3
Bignonia capreolata SE N Amer
Campsis radicans SE N Amer
Chilopsis linearis Son wide

BIXACEAE 1/1
Amoreuxia wrightii Amer Trop/Subtr

BLECHNACEAE 1/1
Blechnum occidentale Amer Trop/Subtr

BORAGINACEAE 11/22
Antiphytum heliotropioides S Chih (Coah)
Cordia podocephala Chih-Tam
Cryptantha mexicana Chih
Cryptantha minima W Prair
Cryptantha palmeri Chih
Cryptantha texana SEC TX endemic
Ehretia anacua Tam
Heliotropium confertifolium Chih
Heliotropium curassavicum Amer
Heliotropium glabriusculum Chih
Heliotropium tenellum E Prair
Heliotropium torreyi Chih-Tam
Lappula redowskii W N Amer
Lithospermum incisum N Amer (C)
Lithospermum matamorense Tam
Lithospermum mirabile S TX endemic
Myosotis verna N Amer (mostly E)
Omphalodes aliena Chih
Onosmodium bejariense Prair (C-E)
Onosmodium helleri Edw Plat
Tiquilia canescens Madr
Tiquilia mexicana Chih

BRASSICACEAE 14/37
Arabis petiolaris S TX endemic
Cardamine macrocarpa Chih
Cardamine parviflora Holarctical
Cardamine pensylvanica N Amer
Descurainia pinnata N Amer (mostly W)
Dimorphocarpa candicans SW Prair
Draba brachycarpa E N Amer (E Prair)
Draba cuneifolia W N Amer (W & SC)
Draba platycarpa W N Amer (W & SC N Amer disj)
Erysimum asperum Prair
Lepidium alyssoides SW N Amer
Lepidium austrinum SC N Amer
Lepidium densiflorum N Amer
Lepidium lasiocarpum W N Amer
Lepidium oblongum N Amer (S & C)
Lepidium virginicum N Amer
Nerisyrenia camporum Chih
Paysonia grandiflora SEC TX endemic
Paysonia lasiocarpa Tam
Physaria argyraea Chih-Tam
Physaria densiflora Comanch (NCE TX)
Physaria engelmannii Comanch
Physaria fendleri SW N Amer
Physaria gordonii Son (+ SW Prair)
Physaria gracilis subsp. *gracilis* Prair (S)
Physaria purpurea Son-Chih
Physaria recurvata Edw Plat

Physaria sessilis Edw Plat
Rorippa curvipes W N Amer
Rorippa sessiliflora E Prair (+ E N Amer)
Rorippa teres Gulf
Selenia jonesii S TX endemic (WC)
Sibara viereckii Tam
Sibara virginica E N Amer
Streptanthus bracteatus Edw Plat endemic
Streptanthus carinatus Son-Chih
Streptanthus platycarpus Edw Plat endemic (W)

BROMELIACEAE 1/2
Tillandsia recurvata Amer Trop/Subtr
Tillandsia usneoides Amer Trop/Subtr

BUDDLEJACEAE 2/2
Buddleja racemosa Edw Plat endemic (S)
Polypremum procumbens Amer Trop/Subtr

CACTACEAE 13/40
Ancistrocactus brevihamatus S TX (SW-SC)
Ancistrocactus scheeri Tam
Ariocarpus fissuratus Chih
Coryphantha echinus Chih
Coryphantha macromeris Chih
Coryphantha sulcata SC N Amer
Cylindropuntia davisii SW N Amer
Cylindropuntia imbricata SW N Amer
Cylindropuntia kleiniae Son-Chih
Cylindropuntia leptocaulis Chih-Tam
Cylindropuntia tunicata Madr (+ S Amer)
Echinocactus horizonthalonius Chih
Echinocactus texensis SC N Amer
Echinocereus coccineus SW N Amer
Echinocereus enneacanthus Chih-Tam
Echinocereus pectinatus Chih-Tam
Echinocereus reichenbachii SC N Amer
Echinocereus stramineus Chih
Echinocereus triglochidiatus SW N Amer
Epithelantha micromeris Son-Chih
Escobaria emskoetteriana E Chih-Tam
Escobaria missouriensis W N Amer (WC)
Escobaria vivipara W N Amer
Ferocactus hamatacanthus Chih-Tam
Glandulicactus uncinatus var. wrightii Chih
Grusonia schottii Chih-Tam
Hamatocactus bicolor Tam
Mammillaria heyderi Son (+ Tam)
Mammillaria lasiacantha Son-Chih
Mammillaria prolifera var.texana Chih-Tam
Mammillaria sphaerica Tam
Neolloydia conoidea Chih-Tam
Opuntia atrispina S TX endemic
Opuntia edwardsii S TX endemic
Opuntia engelmannii Son wide
Opuntia humifusa E N Amer
Opuntia macrocentra Son wide
Opuntia macrorhiza SW N Amer (+ Prair)
Opuntia phaeacantha SW N Amer
Opuntia strigil S TX endemic

CALLITRICHACEAE 1/2
Callitriche heterophylla Amer (C & N)
Callitriche peploides SE N Amer

CAMPANULACEAE 3/9
Campanula reverchonii Edw Plat endemic
Lobelia berlandieri Chih
Lobelia cardinalis N Amer
Triodanis biflora N Amer
Triodanis coloradoensis Edw Plat
Triodanis holzingeri Prair (CS)
Triodanis leptocarpa Prair (E & N)
Triodanis perfoliata N Amer
Triodanis texana Comanch (CE/NC TX endemic)

CAPPARACEAE 3/4
Cleomella angustifolia Prair
Koeberlinia spinosa Amphitrop (Son-Chih)
Polanisia dodecandra N Amer
Polanisia erosa Comanch?

CAPRIFOLIACEAE 4/4
Lonicera albiflora SWC N Amer disj Mont
Sambucus nigra Holarctical
Symphoricarpos orbiculatus E N Amer
Viburnum rufidulum E N Amer

CARYOPHYLLACEAE 7/12
Arenaria benthamii SC N Amer (C-S TX)
Cerastium brachypodum N Amer
Loeflingia squarrosa W N Amer
Paronychia drummondii Comanch
Paronychia jamesii Prairie (W)
Paronychia lindheimeri Edw Plat
Paronychia monticola S TX-Coah
Paronychia setacea CS TX endemic
Paronychia virginica E N Amer disj
Sagina decumbens N Amer
Silene antirrhina N Amer
Stellaria cuspidata Mesoam (+ Andean)

CELASTRACEAE 3/3
Celastrus scandens N Amer (NE-NC)
Mortonia sempervirens Chih
Schaefferia cuneifolia Chih-Tam

CERATOPHYLLACEAE 1/1
Ceratophyllum demersum Polichor

CHENOPODIACEAE 2/8
Atriplex argentea W N Amer
Atriplex canescens W N Amer
Chenopodium berlandieri N Amer
Chenopodium desiccatum W N Amer
Chenopodium incanum W N Amer
Chenopodium leptophyllum W N Amer
Chenopodium pratericola N Amer
Chenopodium simplex N Amer

CISTACEAE 2/4
Helianthemum georgianum SE N Amer (SC-SE)
Lechea mucronata E N Amer
Lechea san-sabeana Comanch (E TX)
Lechea tenuifolia E N Amer

CLUSIACEAE 1/3
Hypericum drummondii E N Amer
Hypericum gentianoides E N Amer
Hypericum mutilum E N Amer

COMMELINACEAE 3/10
Commelina erecta E N Amer
Tinantia anomala Edw Plat endemic
Tradescantia brevifolia S TX (Trans-Pecos)-Coah
Tradescantia edwardsiana C TX endemic

Tradescantia gigantea Comanch (CNE TX)
Tradescantia hirsutiflora E N Amer
Tradescantia humilis SE TX
Tradescantia occidentalis Prair wide
Tradescantia ohiensis E N Amer
Tradescantia pedicellata Edw Plat endemic

CONVOLVULACEAE 6/13

Bonamia repens N Chih
Convolvulus equitans SWC N Amer
Cressa truxillensis Madr
Dichondra carolinensis E N Amer (+ Japan) Amer-Asian?
Dichondra recurvata E Edw Plat endemic
Evolvulus alsinoides Madr
Evolvulus nuttallianus WC N Amer
Evolvulus sericeus Amer Trop/Subtr
Ipomoea cordatotriloba Amer Trop/Subtr
Ipomoea costellata Son
Ipomoea leptophylla Prair
Ipomoea lindheimeri Chih
Ipomoea pandurata E N Amer

CORNACEAE 1/1

Cornus drummondii E Prair

CRASSULACEAE 2/3

Crassula aquatica Amer (N & C) Coastal
Sedum nuttallianum Comanch
Sedum wrightii SWC N Amer (Apach)

CROSSOSOMATACEAE 1/1

Glossopetalon texense Edw Plat endemic

CUCURBITACEAE 5/6

Cucurbita foetidissima Madr wide
Cyclanthera dissecta Mesoam-Madr
Ibervillea lindheimeri SC N Amer-Gulf
Ibervillea tenuisecta Chih
Melothria pendula E N Amer (Gulf)
Sicyos angulatus N Amer (C-NE)

CUPRESSACEAE 2/4

Juniperus ashei Comanch
Juniperus pinchotii SWC USA
Juniperus virginiana E N Amer
Taxodium distichum SE N Amer

CUSCUTACEAE 1/6

Cuscuta cuspidata Prair
Cuscuta indecora N Amer
Cuscuta pentagona Amer
Cuscuta squamata Chih

CYPERACEAE 11/69

Bulbostylis capillaris Amer (Amphipacific)
Bulbostylis juncoides S Mesoam
Carex alata E N Amer (Gulf)
Carex amphibola E N Amer
Carex aureolensis SC US
Carex austrina Prair
Carex brevior N Amer (N & C Prair)
Carex cephalophora E N Amer (NE-NC)
Carex cherokeensis SE N Amer
Carex edwardsiana Edw Plat endemic
Carex emoryi N Amer (C & NE)
Carex microdonta Prair (CS)
Carex muehlenbergii E Prair-E N Amer
Carex perdentata Comanch
Carex planostachys SC N Amer
Cladium mariscus Subtr
Cyperus acuminatus N Amer
Cyperus croceus SE N Amer-C Amer
Cyperus echinatus E N Amer
Cyperus elegans Mesoam-S Amer
Cyperus erythrorhizos N Amer
Cyperus esculentus Amer-Afr (Polichor)
Cyperus flavescens Trop/Subtr/Warm
Cyperus haspan Trop/Subtr
Cyperus hermaphrodites Amer Trop/Subtr
Cyperus lupulinus E N Amer
Cyperus odoratus Amer
Cyperus pseudothyrsiflorus SC USA
Cyperus pseudovegetus E N Amer-C Amer
Cyperus reflexus S Amer-Mesoam
Cyperus retroflexus S N Amer
Cyperus retrorsus SE N Amer-C Amer
Cyperus setigerus S Prair
Cyperus squarrosus Amer-Afr
Cyperus strigosus N Amer
Cyperus thyrsiflorus Amer Trop/Subtr
Eleocharis acicularis Amer
Eleocharis atropurpurea Trop/Subtr/Warm
Eleocharis cellulosa Amer Trop/Subtr
Eleocharis compressa E N Amer (+ Prair)
Eleocharis flavescens Amer Trop/Subtr
Eleocharis geniculata Amer-Afr
Eleocharis interstincta Amer Trop/Subtr
Eleocharis lanceolata SE Prair
Eleocharis montevidensis Amer (N Amer-C Amer)
Eleocharis obtusa N Amer
Eleocharis occulta Comanch
Eleocharis palustris Holarctical
Eleocharis parvula Holarctical
Eleocharis quadrangulata N Amer (E)
Eleocharis rostellata N Amer-C Amer
Fimbristylis autumnalis Amer
Fimbristylis dichotoma Trop/Subtr
Fimbristylis puberula E N Amer (Prair-SE N Amer)
Fimbristylis vahlii Amer Trop/Subtr
Fuirena simplex N Amer-Mesoam
Fuirena squarrosa SE N Amer
Isolepis carinata SE N Amer
Kyllinga brevifolia Trop/Subtr
Lipocarpha aristulata N Amer
Lipocarpha micrantha Amer (+ Afr)
Rhynchospora colorata Carib (Gulf-C Amer-Carib)
Rhynchospora nivea Comanch
Schoenoplectus californicus Amer Trop/Subtr/Warm
Schoenoplectus hallii Prair
Schoenoplectus maritimus W N Amer
Schoenoplectus pungens Polichor
Schoenoplectus saximontanus N Amer (W & C)
Schoenoplectus tabernaemontani Polichor

DENNSTAEDTIACEAE 1/1

Dennstaedtia globulifera Amer Trop/Subtr

DRYOPTERIDACEAE 5/5

Cystopteris utahensis ?
Dryopteris cinnamomea Madr (S & W)
Onoclea sensibilis E N Amer
Tectaria heracleifolia Mesoam (+ N S Amer)
Woodsia obtusa E N Amer

EBENACEAE 1/2
Diospyros texana Chih-Tam
Diospyros virginiana E N Amer

ELATINACEAE 2/2
Bergia texana ? (W N Amer-Prair)
Elatine brachysperma ? (N Amer)

EPHEDRACEAE 1/5
Ephedra antisyphilitica Chih-Tam (+ NE TX, OK)
Ephedra aspera Madr disj
Ephedra pedunculata Chih-Tam
Ephedra torreyana SW N Amer
Ephedra trifurca N Madr

EQUISETACEAE 1/3
Equisetum ×ferrissii ?
Equisetum hyemale Holarctical
Equisetum laevigatum N Amer

ERICACEAE 1/1
Arbutus xalapensis Mesoam

ERIOCAULACEAE 1/1
Eriocaulon koernickianum E N Amer disj

EUPHORBIACEAE 12/68
Acalypha gracilens E N Amer
Acalypha monococca Prair (E)
Acalypha monostachya Madr
Acalypha ostryifolia Amer (C & N Amer)
Acalypha phleoides Madr wide
Acalypha radians S TX (SCE TX)
Acalypha virginica E N Amer
Argythamnia aphoroides Edw Plat
Argythamnia argyraea S TX endemic
Argythamnia humilis S Prair
Argythamnia mercurialina Prair-W Amer
Argythamnia neomexicana N Madr
Argythamnia simulans Edw Plat endemic
Bernardia myricifolia ? Son disj
Bernardia obovata Chih (N)
Chamaesyce acuta Chih (N)
Chamaesyce albomarginata Madr (N)
Chamaesyce angusta S TX (Trans-Pecos-Edw Plat)
Chamaesyce bombensis Gulf (C Amer-Gulf)
Chamaesyce chaetocalyx SW N Amer (Apach)
Chamaesyce cinerascens Chih-Tam
Chamaesyce fendleri WC USA
Chamaesyce glyptosperma N Amer
Chamaesyce hypericifolia Amer Trop/Subtr
Chamaesyce hyssopifolia Amer Trop/Subtr
Chamaesyce jejuna Chih (N)
Chamaesyce lata SWC USA
Chamaesyce maculata E N Amer (+ E Asia)
Chamaesyce missurica Prair
Chamaesyce nutans N Amer (C & E)
Chamaesyce prostrata N Amer (C & N)
Chamaesyce serpens Amer
Chamaesyce serrula Son-Chih
Chamaesyce stictospora N Amer
Chamaesyce villifera Mesoam-Madr
Cnidoscolus texanus SC USA
Croton capitatus E Prair
Croton dioicus Chih-Tam
Croton fruticulosus Chih-Tam
Croton glandulosus Amer Trop/Subtr
Croton incanus E Madr (+ Tam)
Croton lindheimerianus S Prair
Croton monanthogynus E N Amer
Croton pottsii Son-Chih
Croton texensis SWC N Amer
Euphorbia brachycera W N Amer
Euphorbia commutata E N Amer
Euphorbia cyathophora N Amer
Euphorbia dentata N Amer (+ C Amer)
Euphorbia heterophylla N Amer
Euphorbia longicruris SC USA (Comanch?)
Euphorbia marginata Amer
Euphorbia roemeriana Edw Plat endemic
Euphorbia spathulata N Amer
Euphorbia wrightii ? S TX-Coah
Jatropha cathartica Chih-Tam
Jatropha dioica Madr
Leptopus phyllanthoides Comanch
Phyllanthus polygonoides SC N Amer
Stillingia sylvatica SEC N Amer
Stillingia texana SC USA (+ Coah)
Stillingia treculiana E Madr-Tam
Tragia amblyodonta Son Wide
Tragia betonicifolia S Prair
Tragia brevispica Comanch
Tragia leptophylla S TX endemic
Tragia nigricans Edw Plat endemic
Tragia ramosa SWC USA

FABACEAE 41/121
Acacia angustissima Amer Trop/Subtr
Acacia berlandieri Chih-Tam
Acacia constricta Madr wide
Acacia farnesiana Trop
Acacia greggii Madr
Acacia neovernicosa Son
Acacia rigidula Chih-Tam
Acacia roemeriana Chih
Acacia schottii N Chih
Amorpha fruticosa N Amer
Amorpha roemeriana S Edw Plat endemic
Apios americana E N Amer
Astragalus brazoensis S TX-Coah (SCE TX)
Astragalus canadensis N Amer
Astragalus crassicarpus Prair wide
Astragalus lindheimeri Comanch (C TX-Comanch)
Astragalus lotiflorus Prair
Astragalus mollissimus WC N Amer
Astragalus nuttallianus WC N Amer
Astragalus plattensis Prair (W)
Astragalus pleianthus Edw Plat endemic
Astragalus waterfallii Chih
Astragalus wrightii S TX endemic
Baptisia bracteata E Prair
Bauhinia lunarioides Chih
Calliandra conferta Madr (S, C, & E)
Calliandra eriophylla Madr
Centrosema virginianum Mesoam-S Amer
Cercis canadensis E N Amer
Chamaecrista fasciculata E N Amer
Clitoria mariana E N Amer
Dalea aurea Prair
Dalea bicolor Son
Dalea compacta Comanch
Dalea emarginata Tam

Dalea enneandra Prair
Dalea formosa SWC N Amer
Dalea frutescens E Madr
Dalea greggii E Madr
Dalea hallii Comanch (TX endemic)
Dalea laniceps N Chih
Dalea lasiathera Edw Plat (+ S TX-Coah)
Dalea multiflora Prair
Dalea nana Son wide
Dalea pogonathera Son
Dalea polygonoides SW N Amer (disj)
Dalea purpurea N Amer (NC)
Dalea tenuis Comanch
Dalea wrightii Son-Chih
Desmanthus acuminatus SE TX endemic
Desmanthus glandulosus Son-Chih (N)
Desmanthus illinoensis Prair
Desmanthus leptolobus S Prair
Desmanthus obtusus Chih
Desmanthus reticulatus Edw Plat endemic
Desmanthus velutinus Chih
Desmanthus virgatus Amer (except N)
Desmodium lindheimeri Tam
Desmodium paniculatum E N Amer
Desmodium psilophyllum Mesoam (+ E Madr)
Desmodium sessilifolium E Prair
Desmodium tweedyi Comanch
Eysenhardtia texana E Chih-Tam
Galactia canescens Chih-Tam
Galactia heterophylla S TX endemic (CS TX)
Galactia marginalis Amer Trop/Subtr
Galactia texana Edw Plat endemic
Gleditsia triacanthos E N Amer
Hoffmannseggia drepanocarpa SW USA
Hoffmannseggia glauca Amphitrop
Hoffmannseggia oxycarpa Chih
Indigofera lindheimeriana Chih
Indigofera miniata Mesoam-Carib
Lathyrus pusillus ?
Lespedeza stuevei E N Amer (S)
Lespedeza texana Comanch (+ Trans Pecos)
Lespedeza virginica E N Amer
Leucaena retusa Chih
Lotus unifoliolatus N Amer
Lupinus texensis Comanch
Mimosa aculeaticarpa Madr wide
Mimosa borealis SWC USA
Mimosa latidens SE TX (W Gulf)
Mimosa malacophylla Tam
Mimosa nuttallii Prair
Mimosa roemeriana Comanch
Mimosa strigillosa Amphitrop (Gulf-S S Amer)
Mimosa texana Chih
Neptunia lutea SE Prair (+ Gulf)
Neptunia pubescens Mesoam (+ Gulf)
Oxytropis lambertii Prair (+ Roc Mt)
Parkinsonia texana S TX (Tam?)
Pediomelum cuspidatum Prair
Pediomelum cyphocalyx Comanch (NC TX endemic)
Pediomelum humile ? (Val Verde c)
Pediomelum hypogaeum Prair (+ Roc Mt)
Pediomelum latestipulatum Comanch (CN TX)
Pediomelum linearifolium W Prair (+ Roc Mt)
Pediomelum rhombifolium SC US
Pomaria brachycarpa S TX endemic (SC)
Pomaria jamesii S WC USA
Prosopis glandulosa W N Amer (mostly S)
Psoralidium tenuiflorum WC N Amer (Prair-WC)
Rhynchosia minima Trop/Subtr
Rhynchosia senna Amphitrop (Madr-Temp S Amer)
Senna bauhinioides Madr
Senna lindheimeriana Chih-Tam
Senna pumilio Chih
Senna roemeriana SWC USA (NM & W TX)
Senna wislizeni Madr (N & E, disj)
Sesbania drummondii Gulf-Tam
Sesbania herbacea Mesoam
Sesbania vesicaria Gulf
Sophora secundiflora Madr (E)
Strophostyles helvola E N Amer
Strophostyles leiosperma E N Amer (+ W Madr)
Styphnolobium affine Comanch
Tephrosia lindheimeri S TX endemic
Tephrosia potosina Tam
Vicia ludoviciana N Amer (S)
Zornia bracteata Gulf

FAGACEAE 1/17

Quercus buckleyi Comanch
Quercus falcata E N Amer
Quercus fusiformis SC N Amer
Quercus gravesii Chih
Quercus grisea Son wide
Quercus havardii SW Prair
Quercus laceyi S TX endemic
Quercus macrocarpa E N Amer (NE-Prair)
Quercus marilandica E N Amer
Quercus mohriana SWC USA
Quercus muehlenbergii E N Amer
Quercus polymorpha E Madr (+ Mesoam)
Quercus pungens Madr (N & E)
Quercus shumardii E N Amer
Quercus sinuata E N Amer disj
Quercus stellata E N Amer
Quercus vaseyana Chih

FOUQUIERIACEAE 1/1

Fouquieria splendens Son (Son-Chih)

FUMARIACEAE 1/2

Corydalis curvisiliqua Prair (WC)
Corydalis micrantha Prair (E + SE N Amer)

GARRYACEAE 1/1

Garrya ovata S & E Madr

GENTIANACEAE 3/5

Centaurium beyrichii Comanch
Centaurium calycosum E Madr
Centaurium texense Comanch? SE Prair
Eustoma exaltatum Mesoam (+ N Amer)
Sabatia campestris E Prair

GERANIACEAE 2/3

Erodium texanum SWC USA
Geranium carolinianum Amer
Geranium texanum SC US (CE TX-SW LA)

GROSSULARIACEAE 1/1

Ribes aureum N Amer (+ W Europe)

HAMAMELIDACEAE 1/1

Hamamelis virginiana E N Amer

HIPPOCASTANACEAE 1/2
Aesculus glabra E N Amer (Prair-E USA)
Aesculus pavia E N Amer (SE-EC)

HYDRANGEACEAE 2/4
Fendlera rupicola SW N Amer
Fendlera wrightii ?
Philadelphus ernestii Edw Plat endemic
Philadelphus texensis Edw Plat endemic

HYDROPHYLLACEAE 2/7
Nama havardii N Chih
Nama hispidum SWC N Amer
Nama parvifolium Chih-Tam
Nemophila phacelioides Comanch
Phacelia congesta SC N Amer
Phacelia patuliflora SCE TX
Phacelia popei SWC USA

HYPOXIDACEAE 1/1
Hypoxis hirsuta E N Amer

IRIDACEAE 2/4
Nemastylis geminiflora Prair (SE)
Sisyrinchium biforme Gulf (E)
Sisyrinchium minus Prair (SE)
Sisyrinchium pruinosum Prair (SE)

ISOETACEAE 1/2
Isoëtes lithophila Edw Plat endemic
Isoëtes melanopoda N Amer Disj

JUGLANDACEAE 2/6
Carya illinoinensis E N Amer
Carya myristiciformis SE N Amer
Carya texana E Prair
Juglans major Madr wide
Juglans microcarpa SC N Amer
Juglans nigra E N Amer

JUNCACEAE 1/16
Juncus acuminatus N Amer (+ C Amer)
Juncus brachycarpus E N Amer
Juncus bufonius Polichor
Juncus dichotomus Amer Trop/Subtr (Subtr/Warm)
Juncus diffusissimus E N Amer
Juncus dudleyi N Amer
Juncus effusus Polichor
Juncus filipendulus E N Amer disj
Juncus interior Prair
Juncus marginatus Amer
Juncus nodatus E N Amer (E Prair-E N Amer)
Juncus scirpoides E N Amer
Juncus tenuis N Amer, intr els
Juncus texanus E TX
Juncus torreyi N Amer
Juncus validus E N Amer

KRAMERIACEAE 1/4
Krameria erecta Son (mostly W)
Krameria grayi Son
Krameria lanceolata SC N Amer (+ FL)
Krameria ramosissima Tam

LAMIACEAE 11/36
Hedeoma acinoides Edw Plat
Hedeoma drummondii WC N Amer
Hedeoma nana N Madr
Hedeoma reverchonii Comanch
Lycopus americanus N Amer
Monarda citriodora N Amer *(*Prair-SWC)
Monarda clinopodioides Prair (Comanch?)
Monarda fistulosa N Amer
Monarda pectinata SWC USA
Monarda punctata E N Amer
Monarda stanfieldii Edw Plat endemic
Physostegia angustifolia E N Amer (E Prair-SE N Amer)
Prunella vulgaris Polichor
Salvia azurea E N Amer (EC USA)
Salvia ballotiflora E Madr
Salvia coccinea Polichor
Salvia engelmannii Comanch (NCE TX endemic)
Salvia farinacea SC USA (S Prair)
Salvia greggii Chih-Tam
Salvia lyrata E N Amer
Salvia pentstemonoides Edw Plat endemic
Salvia reflexa N Amer (mostly Prair)
Salvia roemeriana Chih
Salvia texana SC N Amer
Salvia whitehousei N Chih
Scutellaria drummondii SC-SE N Amer
Scutellaria ovata E N Amer
Scutellaria resinosa Prair
Scutellaria texana Chih
Scutellaria wrightii SC N Amer (TX-OK)
Stachys crenata SC-SE N Amer
Tetraclea coulteri Son wide
Teucrium canadense N Amer-Mesoam
Teucrium laciniatum SWC USA
Trichostema brachiatum E N Amer
Warnockia scutellarioides Edw Plat (+ SE & NC TX)

LAURACEAE 1/1
Lindera benzoin E N Amer

LEMNACEAE 3/7
Lemna aequinoctialis Polichor
Lemna minor Polichor
Lemna minuta C Amer
Lemna valdiviana Amer
Spirodela polyrrhiza C Amer
Wolffia brasiliensis Amer
Wolffia columbiana Amer

LENTIBULARIACEAE 1/3
Utricularia cornuta E N Amer (+ Carib)
Utricularia gibba Amer-Afr
Utricularia macrorhiza N Amer (N)

LILIACEAE 1/1
Erythronium mesochoreum E Prair

LINACEAE 1/8
Linum berlandieri Prair (SC)
Linum compactum Prair (W & NW)
Linum hudsonioides S Prair
Linum imbricatum SC USA
Linum lewisii W N Amer
Linum pratense SW & SC USA
Linum rigidum W Prair
Linum rupestre Madr wide

LOASACEAE 3/8
Cevallia sinuata Son wide
Eucnide bartonioides Chih-Tam
Mentzelia albescens Amphitrop
Mentzelia lindheimeri Chih-Tam

Mentzelia multiflora SW N Amer
Mentzelia nuda W Prair
Mentzelia oligosperma Prair
Mentzelia reverchonii SC USA

LOGANIACEAE 2/3
Mitreola petiolata Trop/Subtr (Mesoam)
Spigelia hedyotidea Mesoam (+ SC TX)
Spigelia texana SE TX

LYTHRACEAE 4/6
Ammannia auriculata Trop/Subtr-Warm
Ammannia coccinea Mesoam (+ N Amer)
Lythrum californicum W N Amer
Lythrum ovalifolium Edw Plat
Nesaea longipes N Chih
Rotala ramosior Amer

MALPIGHIACEAE 2/2
Aspicarpa hyssopifolia S TX-Chih
Galphimia angustifolia E & W Madr

MALVACEAE 12/24
Abutilon fruticosum Trop
Abutilon parvulum Son
Abutilon wrightii Chih
Allowissadula holosericea Chih-Tam
Callirhoe involucrata Prair
Callirhoe leiocarpa Prair (S, Comanch?)
Callirhoe pedata Comanch
Herissantia crispa Trop/Subtr
Hibiscus coulteri Son wide
Hibiscus laevis E N Amer
Hibiscus martianus Madr (E + Tam)
Hibiscus moscheutos E N Amer
Malvaviscus arboreus Trop/Subtr (Amer)
Meximalva filipes Tam
Modiola caroliniana Amer Trop/Subtr
Pavonia lasiopetala Chih (E)-Tam
Rhynchosida physocalyx Amer Trop/Subtr
Sida lindheimeri SE TX
Sida longipes Chih-Tam
Sida spinosa Amer
Sphaeralcea angustifolia Madr
Sphaeralcea coccinea W N Amer
Sphaeralcea hastulata SW N Amer
Sphaeralcea incana SW N Amer

MARSILEACEAE 2/3
Marsilea macropoda SE N Amer disj
Marsilea vestita N Amer (+ Peru)
Pilularia americana Amer (Warm)

MELANTHIACEAE 2/2
Schoenocaulon texanum Chih
Toxicoscordion nuttallii E Prair

MENISPERMACEAE 2/2
Cocculus carolinus E N Amer
Menispermum canadense E N Amer (NE/EC)

MORACEAE 2/3
Maclura pomifera E N Amer
Morus microphylla SW N Amer (+ SC)
Morus rubra E N Amer

MYRICACEAE 1/1
Morella cerifera Mesoam (+ Gulf)

NAJADACEAE 1/2
Najas guadalupensis Amer
Najas marina Polichor

NELUMBONACEAE 1/1
Nelumbo lutea E N Amer (+ Mesoam)

NYCTAGINACEAE 6/17
Acleisanthes anisophylla Tam
Acleisanthes crassifolia S TX-Coah
Acleisanthes longiflora Son wide
Acleisanthes obtusa E Madr (+ Tam)
Acleisanthes wrightii S TX (SW TX endemic)
Allionia incarnata Amer (mostly SW N & C Amer)
Boerhavia coccinea Trop/Subtr
Boerhavia diffusa Trop/Subtr
Boerhavia erecta Amer Trop/Subtr
Boerhavia linearifolia Chih (+ N NM)
Cyphomeris crassifolia E Chih
Cyphomeris gypsophiloides Chih
Mirabilis albida N Amer
Mirabilis linearis W N Amer (+ Prair)
Mirabilis nyctaginea N Amer-Mesoam
Mirabilis texensis SW TX
Nyctaginia capitata Chih

NYMPHAEACEAE 1/2
Nuphar lutea Holarctical
Nymphaea elegans Mesoam (+ Gulf)

OLEACEAE 3/12
Forestiera angustifolia Chih-Tam
Forestiera pubescens SWC N Amer
Forestiera reticulata E Madr
Fraxinus americana E N Amer
Fraxinus berlandieriana Madr
Fraxinus cuspidata Madr (N & E)
Fraxinus greggii Madr (E Mont)
Fraxinus pennsylvanica E N Amer
Fraxinus texensis Comanch
Menodora heterophylla SE TX
Menodora longiflora SC N Amer
Menodora scabra Madr

ONAGRACEAE 3/24
Calylophus berlandieri SC USA
Calylophus serrulatus Prair
Ludwigia glandulosa E N Amer
Ludwigia octovalvis Polichor
Ludwigia palustris Polichor
Ludwigia peploides Amer
Ludwigia repens E N Amer
Oenothera brachycarpa Madr
Oenothera calcicola E Madr
Oenothera hartwegii SWC USA
Oenothera grandis Prair
Oenothera jamesii SC N Amer
Oenothera kunthiana Mesoam (+ Madr)
Oenothera laciniata Amer, adv els
Oenothera lavandulifolius W N Amer
Oenothera macrocarpa Prair
Oenothera rhombipetala Prair
Oenothera rosea Trop/Subtr (mostly Amer)
Oenothera speciosa N Amer (+ Mesoam)
Oenothera suffulta N Chih
Oenothera suffrutescens W N Amer
Oenothera triloba Prair

Oenothera tubicula N Chih
Oenothera villosa N Amer

OPHIOGLOSSACEAE 1/2

Ophioglossum crotalophoroides Amer
Ophioglossum engelmannii SE N Amer (+ Mesoam)

ORCHIDACEAE 4/7

Corallorhiza wisteriana N Amer
Epipactis gigantea W N Amer
Hexalectris nitida ? (SE NM-S TX)
Hexalectris spicata E N Amer (+ SN Amer)
Hexalectris warnockii S TX? (S AZ-SW/SC TX)
Spiranthes cernua E N Amer
Spiranthes magnicamporum Prair

OROBANCHACEAE 5/13

Agalinis edwardsiana Edw Plat endemic
Agalinis fasciculata SE N Amer (+ Carib)
Agalinis heterophylla SE Prair
Buchnera americana E N Amer
Castilleja genevievana SWC TX
Castilleja indivisa SE Prair
Castilleja lanata Madr
Castilleja purpurea S Prair
Castilleja rigida Chih
Castilleja sessiliflora Prair
Orobanche ludoviciana N Amer
Orobanche multicaulis Madr
Seymeria texana Edw Plat endemic

OXALIDACEAE 1/5

Oxalis albicans Madr wide
Oxalis dichondrifolia E Madr
Oxalis dillenii N Amer
Oxalis drummondii Son-Chih
Oxalis violacea N Amer (mostly E)

PAPAVERACEAE 1/6

Argemone aenea Chih-Tam
Argemone albiflora ssp. *texana* SC US
Argemone aurantiaca Edw Plat
Argemone polyanthemos Prair
Argemone sanguinea E Chih-Tam
Argemone squarrosa SWC USA

PASSIFLORACEAE 1/4

Passiflora affinis E Madr
Passiflora incarnata SE N Amer
Passiflora lutea E N Amer
Passiflora tenuiloba Tam (+ N Chih)

PEDALIACEAE 1/1

Proboscidea louisianica N Amer (mostly S)

PHYTOLACCACEAE 2/2

Phytolacca americana N Amer (mostly E)
Rivina humilis Amer Trop/Subtr

PINACEAE 1/3

Pinus cembroides Madr wide
Pinus edulis SW N Amer
Pinus remota S TX–Coah

PLANTAGINACEAE 11/34

Bacopa monnieri Trop/Subtr/Warm
Bacopa rotundifolia Amer Temp
Leucospora multifida E Prair (+ E N Amer)
Lindernia dubia Amer
Maurandella antirrhiniflora Mesoam (+ Madr)
Mecardonia acuminata SE N Amer
Mecardonia procumbens Amer
Mimulus glabratus Amer
Mimulus guttatus W Amer
Nuttallanthus canadensis N Amer
Nuttallanthus texanus N Amer
Penstemon baccharifolius Chih
Penstemon barbatus SW N Amer
Penstemon buckleyi W Prair
Penstemon cobaea Prair
Penstemon digitalis E Prair (+ NE N Amer)
Penstemon fendleri SWC USA
Penstemon guadalupensis Edw Plat endemic
Penstemon jamesii SW N Amer (Apach)
Penstemon laxiflorus SE Prair (+ W Gulf)
Penstemon triflorus Edw Plat
Plantago aristata E N Amer
Plantago elongata WN Amer (W & C disj)
Plantago helleri SC USA
Plantago heterophylla Amer Temp
Plantago hookeriana SC USA
Plantago ovata Trop/Subtr
Plantago patagonica Amer
Plantago rhodosperma Prair
Plantago virginica E N Amer (+ C Amer)
Plantago wrightiana N Amer (Gulf & SC)
Stemodia schottii ?
Veronica americana N Amer
Veronica peregrina Polichor

PLATANACEAE 1/1

Platanus occidentalis E N Amer

POACEAE 65/199

Achnatherum nelsonii W N Amer
Agrostis elliottiana N Amer (mostly E)
Agrostis hyemalis N Amer
Andropogon gerardii N Amer
Andropogon glomeratus Mesoam
Andropogon virginicus E N Amer (+ C Amer)
Aristida adscensionis Polichor
Aristida desmantha SC USA
Aristida dichotoma E N Amer
Aristida divaricata Mesoam (+ Madr)
Aristida lanosa E N Amer
Aristida longespica E N Amer
Aristida oligantha N Amer
Aristida purpurascens N Amer
Aristida purpurea N Amer (W/C)
Axonopus fissifolius Amer Trop/Subtr
Bothriochloa barbinodis Amer Trop/Subtr
Bothriochloa edwardsiana ? Edw Plat
Bothriochloa hybrida ? (CS TX + SE USA)
Bothriochloa laguroides Amer Trop/Subtr (Subtr)
Bothriochloa longipaniculata Amer Trop/Subtr (Subtr)
Bothriochloa springfieldii Amer Trop/Subtr (Subtr)
Bouteloua aristidoides Amer Trop/Subtr (Subtr)
Bouteloua barbata Amer Trop/Subtr (Subtr)
Bouteloua breviseta Chih
Bouteloua curtipendula Amer
Bouteloua dactyloides Prair wide
Bouteloua eriopoda SWC N Amer
Bouteloua gracilis WC N Amer
Bouteloua hirsuta Prair-N Madr
Bouteloua pectinata Comanch

Bouteloua ramosa N Chih
Bouteloua repens American Trop/Subtr
Bouteloua rigidiseta S Prair
Bouteloua trifida N Madr
Bouteloua uniflora Chih
Bromus pubescens N Amer (mostly E)
Bromus texensis SC TX endemic
Cenchrus echinatus Trop/Subtr
Cenchrus longispinus N Amer
Cenchrus myosuroides Amer Trop/Subtr
Cenchrus spinifex ?
Chasmanthium latifolium E N Amer
Chloris andropogonoides SC TX
Chloris barbata Trop/Subtr
Chloris cucullata SC N Amer
Chloris verticillata Prair (+ W N Amer)
Coelorachis cylindrica SE N Amer
Danthonia spicata N Amer
Dasyochloa pulchella Madr wide
Dichanthelium aciculare SE N Amer (+ Carib)
Dichanthelium acuminatum N Amer (+ Mesoam)
Dichanthelium dichotomum E N Amer (+ C Amer)
Dichanthelium linearifolium E N Amer (NE + Prair)
Dichanthelium oligosanthes N Amer
Dichanthelium pedicellatum Mesoam
Dichanthelium sphaerocarpon E N Amer (+ C Amer)
Digitaria californica Amphitrop
Digitaria cognata E N Amer
Digitaria hitchcockii S TX-Coah
Digitaria insularis Amer Trop/Subtr
Digitaria patens S TX (SW-SC) endemic
Digitaria pubiflora SWC N Amer
Disakisperma dubium SWC N Amer
Distichlis spicata Amer
Echinochloa crus-pavonis Trop/Subtr/Warm
Echinochloa muricata N Amer
Echinochloa walteri E N Amer (+ C Amer)
Elionurus tripsacoides Amer Trop/Subtr
Elymus canadensis N Amer
Elymus elymoides W N Amer
Elymus glabriflorus E N Amer
Elymus interruptus ?
Elymus macgregorii E N Amer
Elymus texensis Edw Plat
Elymus villosus E N Amer (mostly NE)
Elymus virginicus E N Amer
Enneapogon desvauxii Polichor
Eragrostis curtipedicellata SC USA
Eragrostis hirsuta E N Amer
Eragrostis intermedia SWC N Amer
Eragrostis palmeri Chih
Eragrostis pectinacea Amer
Eragrostis secundiflora Amer Trop/Subtr/Warm
Eragrostis sessilispica S Prair
Eragrostis spectabilis N Amer
Eragrostis trichodes N Amer (mostly Prair)
Eriochloa contracta N Amer
Eriochloa sericea Prair (S)
Erioneuron pilosum WC N Amer
Festuca versuta ?
Glyceria striata N Amer
Hesperostipa comata W N Amer
Hesperostipa neomexicana SW USA
Heteropogon contortus Trop/Subtr
Hilaria belangeri Chih
Hopia obtusa SC N Amer (S USA-Madr)
Hordeum jubatum Holarctical
Hordeum pusillum N Amer
Leersia oryzoides Holarctical
Leersia virginica E N Amer (+ Brazil)
Leptochloa fusca Polichor
Leptochloa panicea Trop/Subtr (Amer-Asian)
Limnodea arkansana S Prair (+ Gulf)
Melica montezuma Chih
Melica mutica E N Amer
Melica nitens E N Amer (Appalachian)
Muhlenbergia arenacea Son-Chih
Muhlenbergia arenicola SWC USA (+ Chih)
Muhlenbergia asperifolia Amer (W Temp)
Muhlenbergia dubia Madr Mont
Muhlenbergia ×involuta SC TX (SWC)
Muhlenbergia lindheimeri Edw Plat-Coah
Muhlenbergia porteri Madr (N & WC)
Muhlenbergia pungens SW N Amer (+ W Prair)
Muhlenbergia reverchonii Comanch
Muhlenbergia rigida W Amer Mont
Muhlenbergia schreberi E N Amer (+ S Amer)
Muhlenbergia setifolia Chih
Muhlenbergia sobolifera E Prair (+ NE N Amer)
Muhlenbergia spiciformis Carib
Muhlenbergia tenuifolia Madr
Muhlenbergia utilis Madr
Nassella leucotricha SC N Amer
Neeragrostis reptans Prair (E)
Panicum anceps E N Amer
Panicum brachyanthum SE Prair (+ E Gulf)
Panicum bulbosum Amer
Panicum capillare N Amer (+ Temp S Amer)
Panicum dichotomiflorum Amer
Panicum diffusum Gulf (E TX-Gulf-Carib)
Panicum hallii SWC USA
Panicum hirticaule Amer
Panicum rigidulum E N Amer (+ C Amer-Carib)
Panicum virgatum N Amer
Pappophorum bicolor Madr (E)
Pappophorum vaginatum Amphitrop
Pascopyrum smithii W USA
Paspalidium geminatum Trop/Subtr
Paspalum botterii Gulf (+ Meso Amer)
Paspalum distichum Trop/Subtr/Warm
Paspalum plicatulum Amer Trop/Subtr
Paspalum pubiflorum E N Amer (+ Mesoam)
Paspalum setaceum N Amer (+ C Amer)
Phalaris angusta Amer (coastal)
Phalaris caroliniana N Amer (coastal)
Phragmites australis Polichor
Piptochaetium avenaceum SE N Amer
Pleuraphis jamesii SW USA
Pleuraphis mutica Son wide
Poa arachnifera S Prair
Poa bigelovii N Madr (SWC USA)
Polypogon interruptus Amer (W Amer)
Schedonnardus paniculatus Prair
Schizachyrium scoparium N Amer
Setaria grisebachii Madr-Mesoam
Setaria leucopila SWC N Amer (+ E Madr)
Setaria macrostachya Amer Trop/Subtr
Setaria magna Carib (Amer Subtr)

Setaria parviflora Trop/Subtr/Warm Temp
Setaria reverchonii SC USA
Setaria scheelei Chih-Tam
Setaria texana Tam (+ S TX)
Setaria villosissima Chih
Sorghastrum nutans Amer
Spartina pectinata N Amer (N)
Sphenopholis intermedia N Amer
Sphenopholis obtusata N Amer
Sporobolus airoides W N Amer
Sporobolus clandestinus E N Amer
Sporobolus compositus N Amer
Sporobolus cryptandrus Amer Temp
Sporobolus neglectus N Amer (N)
Sporobolus purpurascens Amer Trop/Subtr
Sporobolus pyramidatus Amer
Sporobolus vaginiflorus N Amer
Sporobolus wrightii Madr
Steinchisma hians Amer Trop/Subtr
Trichloris crinita Amphitrop
Trichloris pluriflora Amer Trop/Subtr
Trichoneura elegans SC TX
Tridens albescens S Prair (SC USA)
Tridens buckleyanus Edw Plat endemic
Tridens eragrostoides Gulf (+ Tam)
Tridens flavus E N Amer
Tridens muticus SWC N Amer
Tridens strictus SE N Amer
Tridens texanus Tam (SC TX)
Triplasis purpurea N Amer (C Amer)
Tripogon spicatus Amer Trop/Subtr (+ S Afr)
Tripsacum dactyloides E N Amer (+ Mesoam)
Trisetum interruptum SWC USA
Urochloa ciliatissima SC USA
Urochloa fusca Amer Trop/Subtr
Urochloa platyphylla Amer Subtr/Warm
Urochloa texana SC N Amer
Vulpia elliotea SE N Amer
Vulpia octoflora N Amer
Zizaniopsis miliacea SE N Amer (+ C Amer)

POLEMONIACEAE 3/9
Giliastrum acerosum SWC USA
Giliastrum incisum Chih wide
Giliastrum ludens SC TX endemic
Giliastrum rigidulum SW C N Amer
Ipomopsis rubra SE N Amer (+ SC N Amer)
Phlox cuspidata Comanch
Phlox drummondii SC USA
Phlox pilosa E N Amer (+ E Prair)
Phlox roemeriana Edw Plat endemic

POLYGALACEAE 1/8
Polygala alba Prair-Madr wide
Polygala barbeyana Madr wide
Polygala lindheimeri Son-Chih
Polygala macradenia Son (+ E Madr)
Polygala ovatifolia Tam N?
Polygala palmeri Chih N?
Polygala scoparioides Son-Chih wide
Polygala verticillata E N Amer

POLYGONACEAE 2/12
Eriogonum annuum Prair
Eriogonum havardii N Chih
Eriogonum longifolium SC USA
Eriogonum multiflorum SC USA
Eriogonum nealleyi S TX endemic
Eriogonum tenellum S Roc M-Chih
Persicaria amphibia Holarctical
Persicaria glabra Polichor
Persicaria hydropiperoides N Amer
Persicaria lapathifolia Polichor
Persicaria pensylvanica N Amer-Mesoam
Persicaria punctata Amer

POLYPODIACEAE 1/1
Pleopeltis polypodioides Amer Trop/Subtr/Warm

PONTEDERIACEAE 1/3
Heteranthera dubia N Amer
Heteranthera limosa Amer
Heteranthera mexicana ?

PORTULACACEAE 3/8
Phemeranthus calycinus Prair
Phemeranthus confertiflorus SWC N Amer
Phemeranthus parviflorus Prair
Portulaca halimoides Amer Trop/Subtr/Warm
Portulaca pilosa Trop/Subtr
Portulaca umbraticola Amer Trop/Subtr
Talinum aurantiacum Madr (E Madr-Apach)
Talinum polygaloides Amphitrop

POTAMOGETONACEAE 1/4
Potamogeton diversifolius N Amer
Potamogeton illinoensis Amer
Potamogeton nodosus Polichor
Potamogeton pusillus Polichor

PRIMULACEAE 2/3
Anagallis minima Polichor
Samolus ebracteatus Mesoam-Madr
Samolus valerandi Polichor

PTERIDACEAE 7/25
Adiantum capillus-veneris Trop/Subtr/Warm
Adiantum tricholepis Mesoam-Madr
Argyrochosma dealbata Prair
Argyrochosma microphylla Son wide
Astrolepis sinuata Amer Trop/Subtr/Warm
Astrolepis windhamii Son
Cheilanthes aemula Tam
Cheilanthes alabamensis E N Amer
Cheilanthes bonariensis Amer-Afr
Cheilanthes eatonii Madr wide
Cheilanthes feei N Amer
Cheilanthes horridula E Madr
Cheilanthes kaulfussii Mesoam
Cheilanthes leucopoda E Madr
Cheilanthes lindheimeri Madr
Cheilanthes tomentosa N Amer (S & SE)
Cheilanthes villosa Son-Chih
Notholaena aschenborniana E Madr
Notholaena copelandii E Madr
Notholaena nealleyi E Madr ?
Notholaena neglecta Chih
Notholaena standleyi Madr (E Madr-Apach)
Pellaea atropurpurea N Amer (+ Mesoam)
Pellaea ovata Mesoam (+ S Amer)
Pellaea wrightiana ? (N Amer sporadic)

RAFFLESIACEAE 1/1
Pilostyles thurberi SW N Amer disj

RANUNCULACEAE 5/11
Anemone berlandieri Amer (SE N Amer/ S S Amer)
Anemone edwardsiana Edw Plat
Anemone tuberosa N Madr
Aquilegia canadensis E N Amer (N)
Clematis drummondii Son
Clematis pitcheri E N Amer
Clematis texensis Edw Plat endemic
Delphinium carolinianum Prair (+ SE N Amer)
Delphinium madrense Chih-Tam
Delphinium wootonii SW N Amer
Ranunculus macranthus SEC TX

RESEDACEAE 1/1
Oligomeris linifolia Madro (N)-Tethyan

RHAMNACEAE 7/13
Berchemia scandens SE N Amer (+ C Amer)
Ceanothus americanus E N Amer
Ceanothus herbaceus Prair
Colubrina texensis Chih
Condalia ericoides Son Mont
Condalia hookeri Tam
Condalia spathulata Tam
Condalia viridis Chih (+ Sonora)
Condalia warnockii Son
Frangula betulifolia Madr wide Mont
Frangula caroliniana SE N Amer
Karwinskia humboldtiana Carib-Son
Ziziphus obtusifolia Madr

ROSACEAE 10/26
Cercocarpus montanus W N Amer
*Crataegus crus-galli*_E N Amer
Crataegus greggiana Tam
Crataegus reverchonii Comanch ?
Crataegus tracyi S TX-Coah
Crataegus turnerorum S TX endemic
Crataegus uvaldensis Edw Plat endemic
Crataegus viridis SE N Amer
Fallugia paradoxa Madr (NC)
Geum canadense E N Amer
Malus ioensis E Prair (mostly NE)
Petrophyton caespitosum W N Amer
Potentilla rivalis W N Amer (+ WC)
Prunus angustifolia SE N Amer
Prunus havardii S TX (Trans-Pecos) endemic Mont
Prunus mexicana E Prair (+ E N Amer)
Prunus minutiflora Edw Plat endemic
Prunus munsoniana E N Amer (+ E Prair)
Prunus rivularis Comanch
Prunus serotina Amer (+ Europe)
Prunus texana SC TX endemic
Rosa carolina E N Amer
Rosa foliolosa Comanch ?
Rubus aboriginum ?
Rubus oklahomus Comanch ?
Rubus trivialis SE N Amer

RUBIACEAE 6/17
Cephalanthus occidentalis N Amer (not C)
Diodia teres Amer
Diodia virginiana E N Amer
Galium aparine Holarctical
Galium circaezans E N Amer
Galium correllii Chih
Galium microphyllum Madr
Galium proliferum N Madr
Galium texense Comanch?
Galium uncinulatum Mesoam
Galium virgatum SC USA (Comanch)
Houstonia acerosa SW N Amer
Houstonia humifusa SC USA
Houstonia pusilla E Prair (+ E N Amer)
Richardia tricocca Madr (mostly E)
Stenaria nigricans E N Amer
Stenaria rupicola N Chih (Trans-Pecos?)

RUTACEAE 3/3
Ptelea trifoliata N Amer (+ Europe)
Thamnosma texana N Son
Zanthoxylum hirsutum Comanch

SALICACEAE 1/1
Populus deltoides Holarctical

SAPINDACEAE 4/4
Cardiospermum halicacabum Trop/Subtr
Sapindus saponaria Trop/Subtr
Serjania brachycarpa Madr (S & E)
Ungnadia speciosa Chih wide?

SAPOTACEAE 1/1
Sideroxylon lanuginosum SE N Amer

SAXIFRAGACEAE 1/1
Lepuropetalon spathulatum SE N (+ S Amer)

SCROPHULARIACEAE 1/2
Leucophyllum frutescens Chih-Tam
Leucophyllum minus Chih

SELAGINELLACEAE 1/8
Selaginella apoda SE N Amer
Selaginella arenicola SE N Amer
Selaginella arizonica Son
Selaginella lepidophylla Madr (E & S)
Selaginella mutica SWC N Amer (Roc Mt)
Selaginella peruviana W Amer
Selaginella underwoodii W N Amer
Selaginella wrightii Chih-Tam

SIMAROUBACEAE 1/1
Castela erecta C Amer (Carib)

SMILACACEAE 1/1
Smilax bona-nox SE N Amer (+ E Madr)

SOLANACEAE 10/28
Bouchetia erecta Madr (E & S)
Chamaesaracha coniodes SC N Amer
Chamaesaracha coronopus SWN Amer
Chamaesaracha edwardsiana ?
Chamaesaracha pallida Chih
Chamaesaracha sordida SWC N Amer
Chamaesaracha villosa Chih
Datura wrightii N Amer (mostly W)
Hunzikeria texana Chih-Tam (E)
Lycium berlandieri Son-Chih
Margaranthus solanaceus Madr
Nicotiana obtusifolia Madr (N + W)
Nicotiana repanda Chih ?
Physalis angulata Amer Trop/Subtr
Physalis cinerascens SC N Amer (+ Mesoam)
Physalis hederifolia SWC N Amer
Physalis longifolia N Amer

Physalis mollis SE N Amer
Physalis pubescens Amer (Polichor)
Physalis virginiana N Amer (E & C)
Quincula lobata SWC N Amer
Solanum citrullifolium Chih?
Solanum dimidiatum S Prair
Solanum elaeagnifolium Amer
Solanum ptycanthum N Amer (mostly E)
Solanum rostratum Prair (+ W N Amer)
Solanum tenuipes Chih
Solanum triquetrum Chih-Tam

STERCULIACEAE 3/3
Ayenia pilosa Chih-Tam
Hermannia texana Tam (+ SC TX)
Melochia pyramidata Amer Trop/Subtr

STYRACACEAE 1/1
Styrax platanifolius S TX-Coah

THELYPTERIDACEAE 1/1
Thelypteris ovata Carib (Gulf-Mesoam-Carib)

THEMIDACEAE 1/1
Androstephium caeruleum Prair

TILIACEAE 1/1
Tilia americana E N Amer

TYPHACEAE 1/2
Typha domingensis Trop/Subtr
Typha latifolia Polichor

ULMACEAE 2/7
Celtis ehrenbergiana Amer Trop/Subtr
Celtis laevigata E N Amer
Celtis lindheimeri Edw Plat endemic
Celtis reticulata W N Amer
Ulmus americana E N Amer
Ulmus crassifolia SC USA
Ulmus rubra E N Amer

URTICACEAE 3/3
Boehmeria cylindrica Amer
Parietaria pensylvanica N Amer
Urtica chamaedryoides Amer

VALERIANACEAE 1/5
Valerianella amarella Comanch
Valerianella florifera SE TX endemic
Valerianella radiata SE N Amer
Valerianella stenocarpa Edw Plat endemic
Valerianella texana Edw Plat endemic

VERBENACEAE 6/13
Aloysia gratissima Amphitrop
Aloysia wrightii Son
Bouchea linifolia Chih (S TX-Coah)
Callicarpa americana SE N Amer
Glandularia bipinnatifida Prair
Glandularia pumila SC USA
Glandularia quandrangulata Chih-Tam
Glandularia tumidula S Edw Plat
Lantana achyranthifolia Mesoam-S Amer
Phyla cuneifolia Prair (WC USA)
Phyla fruticosa Amer Trop/Subtr
Phyla lanceolata Amer Trop/Subtr
Phyla nodiflora Amer Trop/Subtr

VIOLACEAE 2/3
Hybanthus verticillatus SWC USA (+ W Prair)
Viola langloisii ?
Viola sororia E N Amer

VISCACEAE 1/2
Phoradendron hawksworthii N Chih
Phoradendron leucarpum ?

VITACEAE 4/11
Ampelopsis arborea SE N Amer (+ Carib)
Ampelopsis cordata E N Amer
Cissus trifoliata Mesoam (+ S N Amer)
Parthenocissus heptaphylla Edw Plat
Parthenocissus quinquefolia E N Amer
Parthenocissus vitacea N Amer (W & N)
Vitis cinerea E N Amer
Vitis monticola Edw Plat
Vitis mustangensis SC N Amer
Vitis palmata EC N Amer
Vitis rupestris E Prair (E Prair-EC N Amer)

ZANNICHELLIACEAE 1/1
Zannichellia palustris Polichor

ZYGOPHYLLACEAE 3/5
Guaiacum angustifolium Chih-Tam
Kallstroemia hirsutissima Son-Chih
Kallstroemia parviflora Madr (Amphitrop)
Kallstroemia perennans SW TX endemic
Larrea tridentata Madr wide (W)

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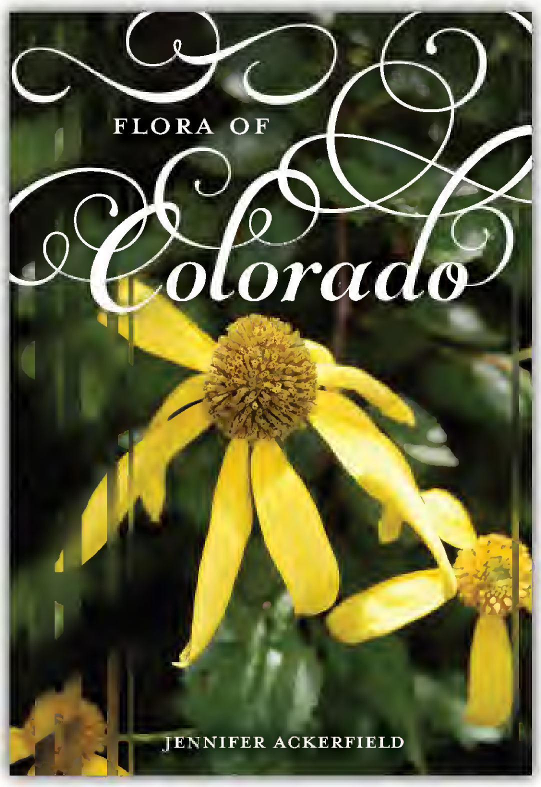
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